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Stable Isotope Study of Food Webs in Lakes of Alberta's Boreal Forest

by

Catherine Patricia Beaudoin

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of
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in

Environmental Biology and Ecology

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This thesis is dedicated, with love, to my

Mom and Dad

Thank you for your unfailing love and encouragement

ABSTRACT

Timber harvesting in Alberta's boreal forest has recently increased. It is imperative to collect pre-harvest data on lakes of the region to evaluate potential logging effects. Stable isotope analysis and fish stomach content analysis were used to characterize food webs and determine the importance of external and internal carbon sources in lakes with different fish assemblages prior to harvesting. Consumers in lakes with water residence times >1 yr primarily used internal carbon inputs, whereas in lakes with water residence times ≤1 yr, consumers primarily used external inputs. Fathead minnows and northern pike were omnivorous and often occupied similar trophic levels. Pike feeding habits were flexible as their prey base changed. A prevalence of omnivory in fish and invertebrates, and the apparent generalist feeding habits of certain fish species, suggests that organisms may be flexible in their feeding habits in the face of altered food webs due to logging.

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Chapter 1. GENERAL INTRODUCTION

Why study food webs?

Lakes are important as water supplies for humans, as well as natural habitats for aquatic organisms (Crowder et al. 1988). Organisms with varied life-histories and feeding habits occupy different habitats within lakes, resulting in lake food webs that can be spatially complex. Limnetic (or pelagic) communities consist of organisms that inhabit the off-shore water of a lake, littoral communities include organisms found along the shoreline, from the edge of the water down to the limits of rooted vegetation, and benthic (profundal or littoral) organisms include those attached to, resting on, or which burrow into the bottom sediments of a lake (Allaby 1994). Despite spatial separation, interactions between organisms within the littoral, limnetic and benthic zones occur (Lodge et al. 1988), all of which contribute to the movement of nutrients (and energy) through the food web in a lake (Crowder et al. 1988).

Food webs are often presented as static snapshots of one location at one time or as a seasonal average and, as such, may be unrealistic representations. Thus, an understanding of temporal food web dynamics is needed in addition to the complex spatial structure. Temporal food web dynamics in lakes depend on the life histories of aquatic organisms, as well as environmental changes that occur seasonally (Crowder et al. 1988). Understanding the complex interactions between organisms within lake food webs and energy flow is essential for effective management of lake ecosystems.

Food webs are often based on the assumption that aquatic systems can be described in terms of discrete trophic levels, such as primary producers (i.e., autotrophs), primary consumers (i.e., herbivores) and secondary consumers (i.e., carnivores). However, discrete trophic levels do not always represent true trophic structure (Kling et al. 1992, Vander Zanden and Rasmussen 1996). In reality, food webs are complex, and omnivory (when organisms consume prey from more than one trophic level, Pimm 1982), is quite common (Vander Zanden and Rasmussen 1996). In recent years, omnivory has been documented in many freshwater ecosystems (e.g., Sprules and Bowerman 1988,

Vadas 1990, Kling et al. 1992). Therefore, when characterizing lake food webs, omnivory cannot be ignored.

Sometimes food webs are depicted in ways that are biased towards the interests of the scientist. Limnologists tend to detail nutrient pathways and organisms in the lower trophic levels and underemphasize invertebrates and fish at the higher trophic levels. In contrast, fisheries biologists tend to focus more on fish and de-emphasize lower trophic levels. These two schools of thought are the origins of contrasting food web theories on the driving forces of trophic interactions in lakes (Crowder et al. 1988). The bottom-up view states that food webs are predominantly driven by the energy sources at the bottom of the food web that flow upward and affect the higher trophic levels (McQueen et al. 1986). The top-down model suggests that higher level consumers, such as fish, exert strong influences on organisms at lower trophic levels (Carpenter et al. 1985). Most researchers now recognize that a combination of bottom-up and top-down effects in lakes operate simultaneously.

Use of stable isotopes in food web studies

Traditionally, there have been three sets of tools used to study food webs: observations of organismal interactions, experimental studies at the mesocosm or ecosystem scale, and analysis of stomach contents. More recently, analyses of naturally occurring stable isotope ratios, especially those of carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N), have become widespread in aquatic ecology to describe food webs. The ratio of a heavy to light isotope of an element in an organism can provide a variety of information useful in food web studies. The alteration of the heavy to light isotope ratio in an organism or material is the result of a process called fractionation, which can occur during biological, chemical, and physical reactions (Peterson and Fry 1987). During trophic interactions, isotopic fractionation often takes the form of enrichment (a relative increase of the heavier isotope in consumers compared with their prey).

The stable isotopic composition of a sample (e.g., an organism) is usually expressed in terms of its difference from a standard reference material. Relative isotopic composition is calculated because of the difficulty in measuring the absolute isotopic

ratio of materials and the precision required for such analyses (Ehleringer and Rundel 1989). The reference material used for nitrogen isotope analyses is atmospheric N_2 and the reference material used for carbon isotope analyses is PeeDee Belemnite (PDB) limestone (Ehleringer and Rundel 1989). The difference between the isotopic composition of a sample and standard is expressed in delta (δ) notation and is calculated (using carbon as an example) as

$$\delta^{13}C = [(R_{sample} - R_{standard})/R_{standard}] \times 10^3$$

where R equals the isotopic ratio, $^{13}C/^{12}C$; R_{sample} refers to the ratio of the sample; $R_{standard}$ refers to the ratio of the reference material. Thus, $\delta^{13}C$ or $\delta^{15}N$ is the relative difference between the ^{13}C and ^{15}N content of the sample, respectively, and that of the standard, expressed as permil (‰).

The complementary use of stable isotope ratios of two or more elements, such as carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), can provide a detailed picture of a food web. Because there is only limited fractionation (0-1 ‰ enrichment) of ^{13}C in a predator relative to its prey (DeNiro and Epstein 1978), $\delta^{13}C$ of organisms generally reflect the isotopic composition of their diet, providing information on the original source of carbon to the food web. For example, there is often a difference between the $\delta^{13}C$ signal of allochthonous and autochthonous carbon sources in a freshwater lake or stream ecosystem and these differences can be traced in the consumers. Generally, the $\delta^{13}C$ signatures of terrestrial material fall between -29 to -26 ‰, whereas autochthonous material is often either relatively more depleted or enriched in ^{13}C, depending on the system (Rau 1980, Rosenfeld and Roff 1992). In the case of nitrogen, $\delta^{15}N$ of consumers consistently become enriched as an organism's trophic position in the food web increases (Hesslein et al. 1991) because organisms preferentially excrete the lighter nitrogen isotope (Minagawa and Wada 1984, Peterson and Fry 1987). The enrichment in $\delta^{15}N$ from prey to predator in food web studies is generally 2 to 5 ‰ (Minagawa and Wada 1984, Peterson and Fry 1987, Fry 1991, Hesslein et al. 1991, Kidd 1995), with an average of 3.4 +/-1.1 ‰ (Minagawa and Wada 1984). Thus, $\delta^{13}C$ and $\delta^{15}N$ provide information on an organism's diet and trophic level, respectively.

In systems where dietary habits of organisms are difficult to determine with conventional techniques, stable carbon and nitrogen isotope ratios can be particularly useful to elucidate food web relationships. Stable isotope analysis provides a history of an animal's diet (i.e., an integrated signal of what is digested and assimilated by an organism over a relatively long period of time). Complexity of trophic interactions can sometimes make it difficult to figure out an organism's diet and trophic level with the use of stable isotope analysis alone. Some ecosystems are complex with many producers and consumers that have variable and/or overlapping isotopic signatures. Also, there is always a possibility of an unknown carbon source at a particular locale (Gearing 1991). Therefore, stable isotope analysis of food webs should be complemented with other data, such as stomach content analyses of consumers and/or physicochemical parameters of the ecosystem, whenever possible (Gearing 1991). In contrast to stable isotope analysis, stomach content analysis provides direct information about what an organism consumed just prior to being caught (Gearing 1991), and thus complements stable isotope analysis. Physicochemical characteristics of the lake can help to interpret isotopic variation of organisms. Although stable isotope analysis is a tool that is potentially powerful, one must be aware of the limitations associated with isotopic variability and/or indistinct isotopic signatures.

Spatial and temporal isotopic variation of primary producers between lakes is common and important to consider. Differences in $\delta^{13}C$ or $\delta^{15}N$ signatures of primary producers in various ecosystems will be reflected in the $\delta^{13}C$ and $\delta^{15}N$ signatures of their respective consumers (Gu et al. 1994, Kidd 1995, Cabana and Rasmussen 1996). For example, the $\delta^{15}N$ signatures of particulate organic matter (POM, consisting of mostly algae) in arctic lakes varied from 1.6 to 3.2 ‰ (Kling et al. 1992). In contrast, POM (mostly phytoplankton) samples from Lake Suwa in Japan ranged from 5.8 to 11.8 ‰ (Toda and Wada 1990). Zooplankton at comparable trophic levels in the two ecosystems had isotopic compositions reflecting the differences in basal $\delta^{15}N$. Interpretation of a consumer's $\delta^{15}N$ relative to a baseline $\delta^{15}N$ provides a continuous measure of the consumer's trophic position, which is very valuable for comparative studies (Vander Zanden et al. 1997).

Within-lake spatial and temporal variations in isotopic signatures of primary producers are also common (e.g., Yoshioka et al. 1989, Toda and Wada 1990, Yoshioka 1991, Gu et al. 1994, Yoshioka et al. 1994, Alexander et al. 1996, and Cabana and Rasmussen 1996). Variability in $\delta^{13}C$ signatures of primary producers is caused by many factors, including carbon source used by the plant, the plant's photosynthetic pathway, and diffusional resistances in the water (Lazerte and Szalados 1982, Cifuentes et al. 1988, Keeley and Sandquist 1992). Variations in $\delta^{15}N$ signatures are also caused by many factors, including various metabolic pathways used for nitrogen assimilation and the relative activity of nitrogen-fixing and denitrifying bacteria (Estep and Vigg 1985, Gu et al. 1996). It is important to consider spatial and temporal variations in isotopic signatures when determining trophic relationships and the importance of allochthonous and autochthonous carbon sources in lakes over space and time to avoid misinterpretations.

Within-year temporal variability of $\delta^{15}N$ of primary producers makes it difficult to determine the baseline $\delta^{15}N$ signature from which to determine trophic levels of higher consumers (Cabana and Rasmussen 1996). The isotopic signature of a large, long-lived primary consumer, such as a mollusk, will integrate the spatial and temporal variation in the $\delta^{15}N$ signatures of primary producers (Cabana and Rasmussen 1996). Also, the mix of primary producers, as assimilated by the primary consumers (which is very difficult to measure directly) is taken into account (Vander Zanden and Rasmussen 1996). Therefore, Cabana and Rasmussen (1996) suggest the use of $\delta^{15}N$ of a widespread, relatively long-lived and large primary consumer, instead of primary producers, as the $\delta^{15}N$ baseline. Vander Zanden et al. (1997) suggest the use of a long-lived primary consumer, such as a mussel, as the $\delta^{15}N$ baseline. Trophic position can be calculated for consumers using the following formula:

$$\text{Trophic position} = [(\text{consumer } \delta^{15}N - \text{mussel } \delta^{15}N)/3.4] + 2;$$

where 3.4 is the trophic enrichment that occurs in $\delta^{15}N$ per trophic level, and 2 is the estimated trophic position of the mussel. The effectiveness of this approach is lake-dependent and it is only useful to determine trophic structure of food webs. Detecting temporal variation of energy sources driving the food web would remain unknown.

Scope of project

Increased forestry activities in the Boreal Plain Ecoregion have raised concerns about the effects of logging on terrestrial, riparian, and aquatic ecosystems in the region. Little research has been conducted on the effects of timber harvesting on lakes of the Boreal Plain (Fisheries and Oceans 1992). The few studies that have been conducted in Canada give a broad assessment of clear-cutting effects on nutrients and hydrological cycles (Nicolsen et al. 1982), and on water quality in streams (Krause 1982, Plamondon et al. 1982). Studies in other regions have indicated various impacts of logging on streams, such as changes in water chemistry and algal flora in Oregon (Hansmann and Phinney 1973, Harr and Fredriksen 1988), changes in water quality, algal species, biomass and primary productivity in small forest brooks of Finland (Holopainen et al. 1991), increases in nutrients as well as water table fluctuation of watersheds (Veery 1986), and increases in inorganic seston in southern Appalachian streams (Gurtz et al. 1980). While it is expected that the impacts found in other regions may be similar in the Boreal Plain, one must account for differences in climate, terrain, forest harvesting techniques, and the biota involved (Fisheries and Oceans 1992).

Lakes of the Boreal Plain Ecoregion are small, shallow, and have relatively long water residence times compared with lakes and streams of other regions of Canada, such as the boreal forest on the Canadian Shield due to lower amounts of precipitation (Mitchell and Prepas 1990, Allan et al. 1994). Additionally, there are few streams in the region, and relatively few fish species are found in these lakes compared with other areas in north-central North America (Tonn and Magnuson 1982, Jackson and Harvey 1989). Low numbers of fish species is partly attributed to the shallowness of the lakes, which when combined with high productivity, can result in low winter oxygen concentrations that are detrimental physiologically to many large-bodied fishes (Tonn and Magnuson 1982, Robinson and Tonn 1989).

Based on studies of logging effects on aquatic ecosystems in the boreal forest on the Shield (Nicolsen et al. 1982), increased export of nutrients, such as phosphorus and nitrogen, to rivers and lakes is expected after logging in the Boreal Plain Ecoregion. Greater inputs of phosphorus are linked to increases in primary production and producers

(Schindler 1978, Prepas and Trew 1983) that may, in turn, contribute to decreased dissolved oxygen concentrations (Babin and Prepas 1985) and alter sizes, species composition, and biomass of invertebrates (Fisheries and Oceans 1992). Oxygen depletion may increase mortality among fishes, especially piscivores such as northern pike, and thus influence community composition in these shallow lakes (Tonn and Magnuson 1982). Increased organic input from the forest may also contribute to increases in phytoplankton biomass and exacerbate decreased dissolved oxygen concentrations. Conversely, suspended organic matter can mitigate increases of phytoplankton biomass due to increased light attenuation and cause a change in phytoplankton species composition (Holopainen et al. 1991). It is imperative to collect base-line data of food web structure in these boreal lakes before harvesting occurs.

The Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) Project was initiated by the University of Alberta in partnership with the Province of Alberta (Alberta Environmental Protection, Economic and Tourist Development, Manning Diversified Forest Products Trust Fund), National Hydrology Research Institute, Alberta-Pacific Forest Industries, Inc. and Weyerhaeuser Canada, Ltd. to address the role of buffer strips in mitigating the impacts of forestry operations in the Boreal Plain Ecoregion. The TROLS study is situated in the aspen-dominated mixed-wood boreal forest of Alberta; both terrestrial and aquatic ecosystems are being studied. Four different widths of buffer strips (20, 100, 200, and 800 m) are being examined. Four study lakes are located in each of three different regions: South Calling Lake, Lac la Biche, and South Pelican Hills. In each region, lakes were assigned to one of the above buffer width treatments. The aquatic portion of TROLS includes core survey work and graduate student projects conducted during a five-year period, two years pre-harvest and three years post-harvest.

My work was conducted during the pre-harvest period of the TROLS project, and encompassed food webs of lakes that supported contrasting fish assemblages. The main objective of my study was to describe and compare the food webs of these boreal lakes prior to timber harvest, providing information about the size or complexity of the different food webs, which is crucial for predicting and understanding any subsequent logging impacts. I used two tools, stable isotope analysis and stomach content analysis,

to evaluate differences among food webs of lakes with large-bodied carnivores or piscivores, those with small-bodied planktivores or omnivores, and those with no fish. I examined, in particular, the diets of northern pike because of the important roles that piscivores can play in the food webs of lakes (Thorp 1986). I also assessed whether allochthonous (external) or autochthonous (internal) energy sources were more important for consumers in the lakes, and whether there were changes in diets and trophic levels of consumers over the summer.

Use of stable isotope analysis has been particularly effective in aquatic ecosystems where the potential energy sources of the food webs are few in number. The lakes of this study are small, eutrophic, and shallow with extensive littoral zones. In contrast to many stable isotope studies, macrophyte biomass is often relatively great, and macrophytes were considered a potential carbon source for consumers in the study lakes. Stable isotope analysis has never been reported for lakes in Alberta's boreal forest, so the effectiveness of this technique for these ecosystems was unknown. The utility of stable isotope analysis in food web studies in these boreal lakes was addressed and evaluated in terms of detecting changes in food webs due to logging.

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Chapter 2. CHARACTERIZATION OF BOREAL LAKE FOOD WEBS PRIOR TO TIMBER HARVESTING BASED ON STABLE ISOTOPE AND STOMACH CONTENT ANALYSIS

Introduction

The effects of logging and the role of buffer strips on water quality and organisms in lakes of the Boreal Plain Ecoregion are unknown. One potential scenario is that logging in Alberta's boreal forest will increase nutrient inputs from the watershed into the lakes. Nutrient increases could enhance phytoplankton biomass (Schindler 1978, Prepas and Trew 1983). In turn, increased phytoplankton biomass can influence aquatic community structure by altering sizes, species composition and biomass of invertebrates, and ultimately fish populations. Increased organic material available for decomposition may also decrease dissolved oxygen concentrations during winter (Babin and Prepas 1985), increasing mortality among fishes, especially large-bodied species (Tonn and Magnuson 1982). A reduction in piscivores can have dramatic effects on prey fish populations (Tonn and Paszkowski 1986) that may, in turn, cause shifts in invertebrate species, which can influence the phytoplankton and epiphyte communities. Thus, logging in a lake's drainage basin could affect communities through nutrient inputs that filter up the food web and/or through changes in top carnivores that cascade down to organisms at lower trophic levels.

Another effect of logging could be to alter sources of energy. The importance of internal and external carbon sources is unknown in lakes of Alberta's boreal forest. Therefore, it is necessary to determine which carbon sources drive lake food webs prior to harvesting so that changes to aquatic communities can be detected. Lakes in Alberta's boreal forest are often small, shallow, and have heavily forested shorelines. Generally, external carbon sources, such as leaves and leaf litter, are of minor importance in lakes, but can be relatively more important in small lakes that are characterized by heavily forested shorelines (Pieczynska 1986). It is expected that in lakes with heavily forested shorelines and relatively short water residence times, external carbon sources will be

important energy sources for organisms. In contrast, in lakes with longer water residence times, internal energy sources are expected to play a large role.

As noted above, if timber harvesting has an impact on food webs in boreal lakes, it could result in changes in fish populations. In the northern boreal forest of Alberta, lakes contain relatively few fish species. This is partly attributed to a paucity of streams in the region and shallowness of the lakes. The shallowness of the lakes, combined with their eutrophic condition, can result in low winter oxygen concentrations that are detrimental to many large-bodied fish (Tonn and Magnuson 1982, Robinson and Tonn 1989). Although there are very few fish species present, a major dichotomy exists in the trophic organization of fish communities (Robinson and Tonn 1989). Some lakes contain piscivores and other large-bodied fishes that are relatively intolerant of hypoxic conditions. Other lakes contain only small-bodied planktivores and omnivores, which are more tolerant of low O_2 conditions (Tonn and Magnuson 1982). Because of this dichotomy, the impacts of forest harvesting on food webs in lakes could thus depend on lake trophic structure.

Reduction of dissolved oxygen to critical concentrations (<1 or 2 mg/L) following logging could exert a greater influence on food webs with populations of large-bodied fish (Casselman and Harvey 1975, Tonn and Magnuson 1982). In contrast, increased phytoplankton biomass or phytoplankton species shifts resulting from increased inputs of nutrients may have a more direct effect on young-of-the-year fish and smaller-bodied omnivorous fish, which use zooplankton as a food source who, in turn, rely on phytoplankton. The characterization of the lake food webs in terms of what organisms are present and how they are trophically linked will provide a framework for assessing potential anthropogenic impacts.

Stable isotope analysis (SIA) and stomach content analysis (SCA) were used to characterize food webs of five boreal lakes. SIA provides information about the foods an animal assimilates over a long period of time, and complements traditional diet analyses such as SCA (Gearing 1991). The ratio of ^{13}C to ^{12}C during trophic transfer changes only 0-1 ‰ and provides information about an organism's diet, whereas the ratio of ^{15}N to ^{14}N increases 3-4 ‰ during trophic transfer and is useful to determine a consumer's trophic

level (Minagawa and Wada 1984; Gu et al. 1994). The use of SIA and SCA should provide a fairly complete view of trophic interactions in these lakes.

Few, if any, food web studies have been conducted on lakes of Alberta's boreal forest with the use of SIA. I tested whether internal energy sources were more important than external sources in lakes with short water residence times ($\leq$ 1 yr), and whether there were differences among food webs in fishless lakes, lakes with large-bodied piscivores, and lakes with small-bodied omnivores or planktivores. This baseline information about trophic structure in low flushing eutrophic lakes, where the balance between sufficient and insufficient dissolved oxygen is precarious for top carnivores, is necessary to assess effects of changes in land use on lake ecosystems.

Materials and Methods

Description of study lakes

The lakes in this study are a subset of 12 lakes from an inter-disciplinary project on the role of buffer strips in the mixed-wood boreal forest of Alberta called TROLS (Chapter 1). Both terrestrial and aquatic ecosystems are being studied, with lakes being a large component of the aquatic study (Chapter 1). Four lakes are located in each of three regions of north-central Alberta: South Pelican Hills (SPH), Lac La Biche (LLB), and South Calling Lake (SCL) (Fig. 2-1). The SPH region is approximately 15 km northwest of the town of Orloff near the eastern boundary of Weyerhaeuser Canada, Ltd.'s Slave Lake Division Forest Management Area. The other two regions are located in Alberta-Pacific Forest Industry, Inc.'s Forest Management Area: LLB is located 45 km north of the town of Lac La Biche, and SCL is approximately 25 km east of the town of Smith. Within each of the three regions, one lake was scheduled to retain a buffer strip of 20-, 100-, 200- and 800-m following harvesting. Thus, names of the lakes were designated based on the region and buffer strip width (e.g., SCL20).

For my study, five of the 12 TROLS lakes were chosen, based on their fish assemblages. SCL20 is a single species lake that contains the fathead minnow (*Pimephales promelas*), a small-bodied omnivore. SPH200 was essentially considered a "pike-only" lake because although a small number of brook stickleback (*Culaea*

inconstans) were introduced in SPH200 briefly in summer 1996 when a beaver dam broke upstream, they were only caught during one sampling period. Two study lakes, SPH20 and LLB20, contain northern pike (*Esox lucius*) along with one or two other fish species. SPH20 has two larger fish species, yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersoni),* along with northern pike. LLB20 contains northern pike and yellow perch. The fifth lake, LLB800, underwent a fishkill in the winter of 1995 and was fishless during the second half of my study. Before the winterkill, LLB800 contained northern pike, yellow perch and white sucker. All the lakes are fairly small, shallow, either eutrophic or mesotrophic (based on mean summer values of total phosphorus, Wetzel 1983), and have water residence times that were less than five years in 1996 (Table 2-1).

Methods

Over the course of my study, five lakes were sampled for fish (if present), invertebrates, and primary producers. Biota in SCL20 ("fathead" lake), SPH200 ("pike-only" lake) and LLB800 ("fishless" lake), were sampled four times between May and September, 1996, to incorporate seasonal changes in the size-and age-distributions of the larger biota, which could alter the food webs. However, fish were not collected in SPH200 during September 1996. Biota in SPH20 ("pike-other" lake) and LLB20 ("pike-perch" lake) were sampled once, in August and September, 1996, respectively. During each sampling, dominant taxa representing all trophic levels, and all potential carbon sources, were collected from several different sites in each study lake so that enough individuals of each taxa were obtained for SIA. Common taxa were also collected in LLB800 (pre-winterkill) and SCL20 during August 1995, but sampling was less intensive compared to 1996.

a) Sampling of aquatic biota and carbon sources

Fish collection in the lakes that contained northern pike, yellow perch and white sucker involved both gillnets and a beach seine during 1996. The number of gillnets set overnight ranged from 5-10 nets depending on the size of the lake. Gillnets were 1.5 x

42.7 m, having 14 different panels with the following barmesh sizes: 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, and 75 mm. In SCL20, the only lake that contained fathead minnows, 10 Gee minnow traps were set overnight at depths of 1-2 m overnight. Upon capture, the total length (TL) of each fish was measured. Northern pike and yellow perch were later separated into two size groups based on their expected feeding habits: >85 mm (large) and ≤85 mm (small) for pike (the length at which pike have been reported to eat only fish) and >150 mm (large) and ≤150 mm (small) for perch (the length at which perch have been documented to begin eating fish) (Frost 1954, Lawler 1965, Clady 1973). Muscle was removed from each fish for SIA either on site and then frozen, or after partial thawing in the laboratory. The digestive tract of each fish was also removed and frozen shortly after collection for stomach content analysis (SCA). Once thawed, stomach contents were examined under a dissecting microscope and sorted taxonomically. Frequency of occurrence for each prey taxon per fish species (or size-class) was calculated as the proportion of stomachs containing the particular prey taxon (Bowen 1996).

Aquatic invertebrates were collected from several locations within each lake. Macroinvertebrates were sampled with a pond net from at least six sites in the littoral zones (two to three sweeps per site). Additional samples of snails, leeches, and other epiphytic invertebrates were collected by hand. Benthic invertebrates in the profundal zone were sampled at three or four sites with an Ekman grab. Live individuals were separated from the detrital fraction and sorted. Trichopterans and mollusks were removed from their cases or shells. For SPH200 ("pike-only" lake), several individual macroinvertebrates of the same taxa collected in June 1996 were analyzed separately to determine isotopic variability among individuals within a taxon. Zooplankton (mostly Cladocera, Copepoda and dipteran larvae) were obtained from vertical hauls of a 243-μm tow net, beginning 1 m above the bottom. Samples from three to four sites were pooled to ensure sufficient biomass for SIA. Zooplankton samples were separated through graded sieves (500 and 243 μm), and further sorted by hand into three groups, Daphnidae (a representative herbivore), Chaoboridae (a representative carnivore) and other

zooplankton. All invertebrates were held in water for at least 24 h to allow them to void their guts.

Phytoplankton samples were obtained from vertical hauls of a 64-μm tow net, beginning 1 m above the bottom. Samples from three to four sites were pooled to ensure sufficient biomass for SIA. Phytoplankton samples were separated through a series of graded sieves (243, 125, and 64 μm). Particulate organic matter (POM) (<64 μm) was collected by filtering water that was passed through a 64-μm phytoplankton net onto a precombusted GF/C filter. Phytoplankton samples were observed under a dissecting microscope to ensure that there was no contamination of zooplankton. However, there may have bee slight contamination of rotifers, which were difficult to separate from phytoplankton in some cases. Periphyton attached to submerged wood was also collected when possible. Emergent, submergent, and floating macrophytes were collected by hand from several sites along the shores of the lakes. Macrophytes were sorted to genus or species and vigorously washed to obtain clean samples of both epiphytes and macrophytes for SIA. Terrestrial samples (leaves of dominant plants, litter, humus, and soil), which were potential external carbon sources, were collected only once by hand from the shores in 1995 for SCL20 and LLB800, and once in 1996 for the remaining lakes. For both aquatic and terrestrial plants, only leaves were used for SIA to decrease within-organism variability (Gearing 1991). Adhering particles or sediments were removed to ensure that all plant and algae samples were clean. Sediment cores were taken from two or three sites in each of the profundal and littoral zones with a four-barrel corer and hand-held corer, respectively. The top 1 cm of detritus from the core was collected for SIA. However, for phytoplankton, epiphytes, and detritus, there was not always sufficient material for SIA.

b) Stable isotope analysis

Following collection, all samples were sorted, purified, processed, and then frozen until further processing for SIA. Once thawed, any material containing a carbonate fraction, which can confound isotopic signatures (Boutton 1991) (e.g., crustaceans, macrophytes), was soaked in 1 N HCl until bubbles no longer appeared to remove

inorganic carbon and then rinsed with deionized distilled water to remove the acid. Because lipids may be depleted in ^{13}C and affect ecological interpretations (Kling et al. 1992), they were removed; samples were washed in a 1:1 methanol:chloroform solution for three 10-min. intervals and then freeze-dried. To homogenize the samples, freeze-dried tissues were ground with a mortar and pestle.

In 1995, samples were analyzed for stable carbon (Boutton et al. 1983) and nitrogen (Kendall and Grim 1990) ratios on a Micromass Optima (TM) dual-inlet isotope ratio mass spectrometer located at the National Hydrology Research Institute (Saskatoon, SK). Samples for carbon analysis were loaded in 9-mm Vycor combustion tubes along with 2 g CuO and one Ag wire that had been purified in open crucibles at 850 °C for 1h. Samples that were difficult to handle (e.g., substances that stuck to the sides of the tubes due to static) were placed in small 6-mm Vycor cuvettes, and carefully slid into the Vycor combustion tubes. All Vycor tubing and reagents were pre-baked at 850 °C for 1 h prior to use. Sample sizes were approximately 4-5 g for fish and invertebrates and 10 mg for phytoplankton, plants, and detritus. For nitrogen isotope analysis, 2 g CuO were loaded into 9-mm Vycor tubes, followed by the appropriate amount of sample (10 g for fish and invertebrates, 15 g for phytoplankton, plants and sediments), 30 times the sample weight of CaO, another 2 g CuO, and 3 g Cu. CuO and CaO were purified in open crucibles at 850 °C for 1 h. Samples were evacuated to at least 1E-3 mb by rotary and diffusion pumping, sealed, and combusted in a muffle furnace at 850 °C for 2 h. Care was taken to ensure that the sample and CuO and CaO were well mixed in the tube, and that the CuO was distributed evenly along the length of the combustion tube. Following combustion, samples were slowly cooled (1°C/min.) to room temperature. The CO_2 or N_2 from the combusted samples were analyzed on a Micromass Optima mass spectrometer within a week of combustion. The external reproducibility was better than +/- 0.1 ‰ for both carbon and nitrogen.

All 1996 samples were analyzed for stable carbon and nitrogen ratios with a Micromass Optima continuous flow mass spectrometer (CF-IRMS) directly coupled to a Carlo Erba NA1500 elemental analyzer (EA) and Autosampler at the National Hydrology Research Institute (Saskatoon, SK). For fish and invertebrates, 1 mg of sample was used,

whereas 2 mg were used for phytoplankton, sediments, and aquatic and terrestrial plants. The freeze-dried and powdered samples were loaded into 5x8 mm tin capsules, which were then folded, crushed into a cube and loaded onto the autosampler of the EA. Samples were flash combusted at 1100 °C, followed by on-line removal of water and on-line chromatographic separation of N_2 and CO_2. The N_2 and CO_2 were introduced directly into the mass spectrometer via helium carrier gas. A pulse of N_2 reference gas was introduced into the mass spectrometer with an automated gas injection system, followed by the N_2 sample gas peak. After integration of the N_2 sample and reference isotopic ratios, the mass spectrometer peak jumps to CO_2 tuning and then integrates the sample CO_2 pulse, followed by an injection of CO_2 from the reference gas box. The total time for measurement of nitrogen and carbon isotope ratios from the same sample is about 9 min. A laboratory working standard of urea was run every 10 samples for the CF-IRMS. External reproducibility of the CF-IRMS instrument for both carbon and nitrogen isotope analysis was better than +/- 0.6 ‰.

Stable isotope data are presented as the relative difference between ratios of the sample and standard gases. A differential notation known as the delta (δ) notation is used to express these relative differences: $\delta R(‰) = [(R_{sample}/R_{standard})/R_{standard}] \times 10^3$, where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $\delta^{13}C$ or $\delta^{15}N$ is the permil (‰) deviation of that sample from the recognized isotope standard, PeeDee Belemnite (PDB) limestone for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$ (Gearing 1991). Calibrations were made with the use of stable isotope reference materials provided by the International Atomic Energy Agency in Vienna, Austria.

Results

a) Lake food webs and carbon sources

Categories for invertebrates were based on expected 3-4 ‰ trophic enrichment of ^{15}N and 0-1 ‰ enrichment of ^{13}C per trophic level (Minagawa and Wada 1984, Gu et al. 1984). Abbreviations for invertebrates in all figures of Chapter 2 can be found in Table 2-2. The 3-4 ‰ expected trophic enrichment in $\delta^{15}N$ of predators (fish and invertebrates) relative to potential prey was usually, but not always evident. Intermediate $\delta^{15}N$

signatures suggested that both fish and invertebrates consumed organisms from more than one trophic level.

Fishes

Based on SIA, fatheads were the top predator in the lake food web with several littoral and pelagic invertebrate taxa as likely prey, and were possibly cannibals (Figs. 2-2a-d). SCA confirmed that fathead were eating chironomid larvae, nematodes, and parts of fatheads, but detritus was the food item most frequently consumed (Table 2-3). Despite their high trophic position in the SIA food web, fathead minnows in SCL20 were omnivorous.

In SPH200 ("pike-only" lake), large northern pike were, not surprisingly, the top aquatic predator. The range in pike $\delta^{15}N$ signatures was large with large pike occupying a higher trophic level than small pike (Fig. 2-3b). Based on SIA, the diets of large northern pike consisted of smaller pike and littoral predacious invertebrates, such as Odonata, Notonectidae, and Hirudinea (Figs. 2-3a-c). SCA supported SIA, indicating that Amphipoda, Odonata (both Anisoptera and Zygoptera) and small fish were food items eaten most frequently by large pike (Table 2-3), including brook stickleback during the August 1996 sampling. Based on SIA, small pike fed potentially on a combination of invertebrates from the littoral zone (Fig. 2-3b). SCA indicated that small northern pike consumed Amphipoda most frequently (Table 2-3). The brook sticklebacks that appeared in June were more enriched in ^{15}N and more depleted in ^{13}C relative to the small northern pike, which suggested various zooplankton were contributing to their diet (Fig. 2-3b). SCA were not performed on brook stickleback. Therefore, if one assumes zooplankton were off-shore (pelagic) organisms and macroinvertebrates were littoral organisms, large and small northern pike relied on littoral food sources, whereas brook stickleback relied on pelagic organisms as well.

In LLB20 ("pike-perch" lake), large northern pike and large yellow perch had similar diets that consisted primarily of littoral invertebrates (Fig. 2-4). Slightly higher $\delta^{15}N$ signatures of large pike relative to large perch suggested that the pikes' diets included some fish as well as invertebrates. Isotopic signatures of small perch were more

enriched in ^{15}N and more depleted in ^{13}C than large perch, suggesting that the former consumed some pelagic prey, including various zooplankton and *Chaoborus* sp. (Fig. 2-4). SCA confirmed that fish (mostly pike) were consumed by large pike, but amphipods had the highest frequency of occurrence in pike stomachs (Table 2-3). Amphipods, as well as chironomids, were also frequent food items for both size-classes of perch with zooplankton present in small perch stomachs (Table 2-3). As in SPH200, large-bodied fish in LLB20 relied heavily on littoral invertebrates, with northern pike eating pike and perch as well, whereas the diets of small yellow perch consisted of pelagic invertebrates.

In SPH20 ("pike-other" lake), $\delta^{15}N$ signatures of the fish species were 3-4 ‰ higher than the signatures of the same species in other lakes (Table 2-4), suggesting they occupied a higher trophic level. Large pike and small perch were caught in SPH20, but the other size-classes of pike and perch were not. Large pike were the top predators, followed by small perch and then white sucker (Fig. 2-5). The isotopic signatures of large pike were consistent with a diet of white sucker and perhaps small pike and invertebrates such as Erpobdellidae (Fig. 2-5). SCA indicated that pike in SPH20 consumed a higher number of invertebrate and fish taxa (12) compared with pike in LLB20 (6 taxa) and SPH200 (9 taxa) (Table 2-3). According to SCA, pike in SPH20 consumed both pike, perch, and fish that were unidentified (perhaps white sucker). As in LLB20 ("pike-perch" lake), the mean $\delta^{13}C$ signature of small perch in SPH20 was 3 ‰ more depleted than pike and sucker, suggesting a greater consumption of pelagic invertebrates than littoral invertebrates (Fig. 2-5), which was consistent with SCA (Table 2-3). Amphipods, chironomids and chaoborids were frequent prey items for small perch in SPH20 (Table 2-3). The isotope signatures of the two white suckers collected failed to clearly identify their food sources, and both stomachs contained only detritus (Table 2-3). Thus, according to SIA and SCA, invertebrates were large components of each fish species' diet, with fish being important for pike as well.

In LLB800, only one small yellow perch (61 mm) was caught in the gillnets during the June sampling in 1996, indicating that the lake was all but fishless. Instead, tadpoles appeared to be abundant. Based on SIA, the perch's diet consisted of a combination of invertebrates, and the tadpoles appeared to be omnivores with diets

consisting of invertebrates and primary producers (Fig. 2-6b). Prior to winter 1996, northern pike, yellow perch, and white sucker were present in LLB800, but disappeared due to a fishkill that winter. Based on $\delta^{15}N$ signatures in 1995, large pike were at the highest trophic level in the food web, followed by perch and sucker (Fig. 2-7b). Based on SIA, large pike appeared to eat other pike and white sucker, as well as invertebrates, whereas both yellow perch and white sucker appeared to have diets consisting of various invertebrates (Fig. 2-7b).

Invertebrates

In all five study lakes, $\delta^{15}N$ signatures indicated the following categories of invertebrates: carnivores, omnivores, and herbivores. Not all lakes contained the same number of invertebrate taxa, but most taxa were common to two or more lakes. The ranges of $\delta^{15}N$ signatures of invertebrate taxa were relatively small (5.2 to 10.1‰) in some lakes (Fig. 2-2d), compared with others (4.0 to 12.8‰) (Fig. 2.5). Assuming 3-4 ‰ enrichment of a consumer relative to its prey (Minagawa and Wada 1984), there were relatively few invertebrate taxa whose isotopic signatures unambiguously indicated that they were solely carnivorous in all lakes. Invertebrates that had higher $\delta^{15}N$ values consistent with diets composed predominantly of other invertebrates in most of the study lakes included Erpobdellidae, Glossiphonidae and larvae of the following Trichoptera: Molannidae (*Molanna* sp.), and Glossosomatidae (Figs. 2.2-2.5). Many invertebrates had isotopic signatures that suggested they consumed invertebrates, but their isotopic signatures were intermediate between signatures of carnivorous and herbivorous invertebrates, which suggested that they may have been feeding from more than one trophic level. The diets of these omnivorous invertebrates appeared to include a combination of invertebrates, primary producers and/or detritus. The omnivorous invertebrates included Dytiscidae, Gyrinidae, Hydrophilidae, Corixidae, Notonectidae (*Notonecta* sp.), Planorbidae (*Helisoma* sp.), Lymnaeidae (*Lymnaea* sp.), Physidae (*Physa* sp.), Oligochaetae, Amphipoda (*Gammarus* sp. and *Hyallela* sp.), Hydrachnidia, Daphnidae (*Daphnia* sp.), Copepoda, zooplankton, and the following insect larvae: Coleoptera, Anisoptera, Zygoptera, Rhyacophilidae, Phryganeidae, Limnephilidae,

Chaoboridae (*Chaoborus* sp.), and Chironomidae. Like the carnivorous invertebrates, there were very few invertebrates that consistently had low $\delta^{15}N$ signatures suggesting diets of primary producers in all lakes. However, the following taxa appeared to be herbivorous: Chrysomelidae, Lymnaeidae, and Ephemeroptera (Caenidae).

The ranges in $\delta^{13}C$ signatures of all invertebrates within each lake varied, from approximately 5 ‰ (-26.1 to 31.0 ‰) in SPH200 ("pike-only" lake) during May 1996 (Fig. 2-3a) to over 14 ‰ (-14.5 to -26.7‰) in LLB800 ("fishless" lake) during June 1996 (Fig. 2-6b). Nevertheless, most $\delta^{13}C$ values of the various taxa fell between -30 and -20 ‰. However, the $\delta^{13}C$ signatures of certain gastropod families (Lymnaeidae and Planorbidae) were sometimes more enriched in ^{13}C relative to the other invertebrates (greater than -20 ‰) (Figs. 2-5, 2-6a-c, 2-7b), suggesting an unidentified carbon source. Also, the $\delta^{13}C$ signatures of certain pelagic organisms were sometimes more depleted than the others (lower than -30 ‰) (Figs. 2-2b,d, 2-3a-c, 2.4), suggesting yet another carbon source.

Primary producers

SIA provided evidence that phytoplankton (composed primarily of five major taxonomic groups, chlorophytes, chrysophytes, cryptophytes, cyanophytes, and diatoms (TROLS core 1996)), particulate organic matter (POM) composed of internally produced matter, and/or epiphytes were potential food sources for certain invertebrates in all but one of the study lakes. In LLB20, the lake with the shortest water residence time, the phytoplankton was too enriched in ^{13}C to be a food source for any consumer (Fig. 2-4). Although, *Polygonum* sp. was a potential food source, POM that was most likely composed of terrestrial matter may have been a food source for Amphipoda (Fig. 2-4). In LLB800, POM was a likely food source for Daphnidae (Fig. 2-6b). Also in LLB800, phytoplankton of several different size-fractions appeared to be consumed by Chironomidae in May (Fig. 2-6a) and Lymnaeidae, Planorbidae, Physidae and zooplankton in August (Fig. 2-6c). During the August sampling of SCL20, epiphytes seemed to be a more likely food source for some invertebrates (e.g., Phryganeidae, Corixidae) than POM (Fig. 2-2c). Epiphytes also appeared to be a potential food source

in SPH200 for littoral invertebrates such as Chironomidae, Phryganeidae, Planorbidae and Caenidae (Fig. 2-3b). Finally, as noted above, unidentified carbon sources, perhaps bacteria or a carbonate mineral ingested along with prey items, may have been used by some consumers.

Although many macrophyte genera had isotopic signatures that were either too enriched or too depleted to be food sources, SIA did suggest that certain macrophyte species were consumed by invertebrates. In SCL20 ("fathead" lake), *Scirpus* sp. may have been a food source for Phryganeidae and Corixidae (Fig. 2-2c). *Nuphar* sp. was a possible food source, in combination with other primary producers such as epiphytes, detritus, *Polygonum* sp., and *Scirpus* sp., for invertebrates like Amphipoda, Corixidae, and Phryganeidae (Figs. 2-2b-d). In SPH200 ("pike-only" lake), *Sagittaria* sp. and *Polygonum* sp. were potential food sources for several invertebrate taxa (Figs. 2-3c,d). *Nuphar* sp. may also have been a food source, in combination with a depleted carbon source, such as epiphytes or terrestrial matter, for Planorbidae (Fig. 2-3a), Lymnaeidae, Chironomidae, and various Trichoptera (Fig. 2-3d). In LLB20 ("pike-perch" lake), the isotopic signatures of *Polygonum* sp. suggested that it may have been a food source for Amphipoda (in combination with a more depleted carbon source such as terrestrial matter) (Fig. 2-4). In SPH20 ("pike-other" lake), the isotope signatures of the floating macrophytes *Lemna* sp., *Sagittaria* sp., and *Polygonum* sp. indicated that they may have been food sources for amphipods and hydrophilid beetles (Fig. 2-5). Also, green algae, such as *Rhizoclonium* sp. and *Gloeotrichia* sp., were potential food sources for Lymnaeidae, if consumed along with epiphytes (Fig. 2-5). In LLB800 ("fishless" lake), most of the macrophytes had $\delta^{13}C$ values that were within the range of the various invertebrates which suggested that they may have been eaten in combination with other macrophytes or with POM. Therefore, most macrophytes that were potential food sources were likely consumed in combination with other items in all five study lakes.

The $\delta^{13}C$ signatures of profundal detritus were constant in all the study lakes, ranging from -32.0 to -29.0+/-0.2 ‰ (Figs. 2.2-2.6). In contrast, the $\delta^{15}N$ signatures were more variable and ranged from 0.9 to 5.2 ‰ (Figs. 2.2-2.6). With one exception, the isotopic composition of profundal detritus in lakes suggested it was of aquatic origin. In

LLB20 (shallow, short water residence time), the isotopic composition of profundal detritus was very similar to that of terrestrial matter (aspen and large organic debris) (Fig. 2-4). SIA indicated that profundal detritus was a potential food source for chironomids and amphipods in LLB20 (Fig. 2-4). Profundal detritus was also a possible food source for zooplankton in SCL20 ("fathead" lake) (Figs. 2-2b,c), and for Chironomidae, and perhaps Chaoboridae and Daphnidae, in SPH20 ("pike-other" lake) (Fig. 2-5). Profundal detritus appeared to be a food source for consumers in SCL20, SPH20 and LLB20, but not in the remaining two study lakes.

Littoral detritus may have been of terrestrial origin in some of the study lakes during some sampling periods. In LLB20 (shallow, short water residence time), littoral detritus had a similar isotopic composition to POM and large organic debris from the littoral zone, and appeared to be a potential food source for amphipods only (Fig. 2-4). In SCL20 ("fathead" lake), littoral detritus was a potential food source for Amphipoda, Corixidae, Hydrophilidae, Limnephilidae and Phryganeidae (Figs. 2-2a,c,d). Littoral detritus was also a potential food source for Corixidae, Hydrophilidae, Amphipoda, Limnephilidae, Planorbidae, and Physidae in SPH200 ("pike-only" lake) (Figs. 2-3c,d). In LLB800, littoral detritus did not appear to be of terrestrial origin but of aquatic origin instead, and was a potential food source for various invertebrates such as Corixidae, Chironomidae, and Amphipoda (Figs. 2-6a,d). However, detritus from the littoral zone did not appear to be used by invertebrates in the remaining study lake, SPH20.

Terrestrial inputs were potential energy sources for the food webs of LLB20 ("pike-perch" lake) (Fig. 2-4) and SPH200 ("pike-only" lake) (Figs. 2-3b,d), the two lakes with the shortest water residence times. In LLB20, the $\delta^{15}N$ and $\delta^{13}C$ signatures of litter and aspen leaves indicated that they could be potential food sources to amphipods and chironomids (Fig. 2-4). Terrestrial matter may have been a source for Chironomidae, Amphipoda, Corixidae, and Physidae in SPH200 during June and September (Figs. 2-3b,d) as well. However, the $\delta^{15}N$ or $\delta^{13}C$ signatures of the terrestrial matter were too depleted to suggest it was an energy source for invertebrates in the three lakes with longer water residence times, SCL20 ("fathead" lake), SPH20 ("pike-other" lake), and LLB800 ("fishless" lake) (Figs. 2-2, 2-5, 2-6).

In two of the deeper lakes, SPH20 ("pike-other" lake) (Fig. 2-5) and SPH200 ("pike-only" lake) (Figs. 2-3a-c), there was a distinction between the energy sources for pelagic and littoral organisms. Pelagic organisms tended to be more depleted in ^{13}C when compared with littoral organisms. In SPH200, $\delta^{13}C$ signatures suggested that northern pike were at the top of the littoral food chain. In contrast, brook stickleback, with $\delta^{13}C$ signatures between those of the littoral and pelagic, were members of both littoral and pelagic food chains. The pelagic food chain appeared to be driven by phytoplankton, whereas the littoral food chain was driven by other primary producers, possibly epiphytes (Figs. 2-3b,c). There was also a tendency for pelagic invertebrates to be more depleted in ^{13}C than littoral invertebrates in SPH20 (Fig. 2-5), although separation between littoral and pelagic food chains was not as apparent as in SPH200.

b) Diet and trophic level changes in organisms at one sampling period

The isotopic variation of several fish and invertebrate taxa within a lake at a particular sampling time period were analyzed. In SCL20, the variation in signatures (both $\delta^{15}N$ and $\delta^{13}C$) of individual fish was usually less than or equal to 3 ‰ (Table 2-5). Variation in isotopic signatures of pike within a size-class in SPH200 was also generally less than 3 ‰, except in August, when ranges in $\delta^{13}C$ and $\delta^{15}N$ for large pike were both just under 5 ‰ (Table 2-5), suggesting some variability in diet and trophic level. For all invertebrate taxa examined except Corixidae, the variability in $\delta^{13}C$ values was slightly greater than $\delta^{15}N$ signatures (Table 2-6), suggesting variability in diet, but not in trophic level. The amount of variability in isotopic signatures between individuals of the same taxon differed depending on the taxon, but variability in $\delta^{13}C$ was usually larger than $\delta^{15}N$.

c) Diet and trophic level changes in organisms over time

Within-year variation during 1996

Two of the three lakes sampled multiple times over the summer 1996, SCL20 ("fathead" lake) and SPH200 ("pike-only" lake), contained fish. In both lakes, the fish remained at the top of the food web all summer (Figs. 2-2a-d and 2-3a-c). Mean $\delta^{15}N$ and

$\delta^{13}C$ signatures remained fairly constant throughout the summer (Table 2-5). Based on SCA, detritus and seeds were always the most frequent prey items for most fathead minnows in SCL20 throughout the summer, except in August when amphipods were consumed more frequently (Table 2-7). In SPH200, invertebrates (amphipods and odonates) were the most frequent diet items for large pike throughout the summer, but a greater diversity of invertebrate taxa were found in pike stomachs in August than earlier in the summer (Table 2-7). In the two intensively studied lakes with fish, there was little variation in mean isotopic signatures of fish, but slight seasonal variation was apparent in their stomach contents.

Up to 15 invertebrate taxa were collected on at least three occasions in the three lakes that were sampled four times in 1996: SCL20 ("fathead" lake), SPH200 ("pike-only" lake), and LLB800 ("fishless" lake). In all three lakes, $\delta^{13}C$ signatures of invertebrates were more variable over the summer than $\delta^{15}N$ signatures (Table 2-8). Ranges in $\delta^{15}N$ of invertebrates in all three lakes were less than 4 ‰ over the four sampling times (Table 2-8). In all lakes, ranges of $\delta^{13}C$ signatures could be small (e.g., zooplankton in LLB800), indicating little change in diet, or large (e.g., Phryganeidae in SCL20), indicating more variety in diet, but not entirely shift trophic levels (Table 2-8). Although diets of invertebrates sometimes varied over the summer, the trophic level they occupied did not (maximum range in $\delta^{15}N$ was 3.8 ‰ , Table 2-8).

The variability in both $\delta^{13}C$ and $\delta^{15}N$ signatures of some primary producers in these lakes was small over time, whereas others varied greatly (more than those of consumers). Variation in isotopic signatures of POM in SCL20 ("fathead" lake) was fairly small (Table 2-9), suggesting that the material composition of POM was consistent over the summer. The range in $\delta^{13}C$ for POM in LLB800 was also small, but $\delta^{15}N$ was more variable (Table 2-9), although this may have been due to zooplankton contaminating some samples. In contrast, the $\delta^{13}C$ signatures of phytoplankton in SCL20 had a large seasonal range (11.8 ‰), whereas the range in $\delta^{15}N$ was relatively small (3.4‰) (Table 2-9), suggesting changes in carbon sources (from CO_2 to HCO_3 or CO_3) but little change in nitrogen base. Among the macrophytes, *Nuphar* sp. was found consistently over the summer in all three lakes. In SCL20, *Nuphar* sp.'s isotopic

signature was quite variable throughout the summer, yet in LLB800 and SPH200, the seasonal variability was relatively small (Table 2-9). The ranges in isotopic signatures of *Potamogeton richardsonii* and *Sagittaria* sp. were also small in LLB800, whereas the ranges in isotopic signatures of *Ceratophyllum* sp. and *Potamogeton zosteriformis* in SPH200 were large (Table 2-9). Finally, the $\delta^{13}C$ and $\delta^{15}N$ signatures of profundal detritus changed little over time in all lakes, varying by less than 1 and 3 ‰, respectively. Thus, variability in isotopic signatures of primary producers appeared to differ according to species and the lake in which they were collected.

Between-year variation during 1995 and 1996

Fish and invertebrates were collected, when present, in both 1995 and 1996 from two lakes, SCL20 ("fathead" lake) and LLB800 (lake that became "fishless"). In SCL20, isotopic signatures of fathead minnows were similar in the two years, suggesting similar diets from year-to-year (Figs. 2-2c and 2-7a). In LLB800, the fish disappeared between August 1995 and the 1996 samplings likely due to winterkill, and the prevalence of tadpoles following the fishkill noticeably increased. In both SCL20 and LLB800, more invertebrate taxa were collected in 1996 than in 1995. A greater diversity of invertebrate taxa during 1996 in LLB800 may have been due to the absence of fish following the winterkill. However, invertebrate richness was also higher in 1996 than 1995 for SCL20; in both lakes, sampling was more intense during 1996. The trophic level of most invertebrates sampled in the food webs of both lakes in 1995 and 1996 remained similar (Figs. 2-2c, 2-7a, 2-6c, 2-7b).

Due to less intensive sampling in 1995, comparisons of primary producers in 1995 and 1996 were limited. Among macrophytes in SCL20 ("fathead" lake), $\delta^{13}C$ values did not vary greatly from year-to-year. *Nuphar* sp. was a great deal more depleted in ^{15}N in the summer of 1995 than in 1996, whereas *Potamogeton* sp., littoral and profundal detritus were just slightly more depleted in 1995 than 1996 (Figs. 2-2c, 2-7a). Profundal detritus in SCL20 may have contributed to the diets of zooplankton in SCL20 in 1996, but did not appear a potential food source in 1995. In LLB800, phytoplankton seemed to be the most likely carbon source at the base of the food web in 1996 (Fig. 2-6c), whereas

there was an unknown carbon source at the base of the food web in summer 1995 (Fig. 2-7b). In SCL20, the carbon and nitrogen isotopic signatures of POM were more depleted and enriched, respectively, in 1995 than in 1996 (Figs. 2-2c, 2-7a), although it was too depleted in ^{13}C to be a food source of invertebrates in either year. In 1996, epiphytes were likely the carbon source driving the food web of SCL20, but the major carbon source in 1995 was unknown (Figs. 2-2c, 2-7a). Terrestrial sources of carbon were not important for any of the organisms in LLB800 or SCL20 in either year. So, in both LLB800 and SCL20, although one carbon source in 1995 was unidentified, more intensive sampling in 1996 identified phytoplankton and epiphytes as the likely carbon sources.

Discussion

With the exception of SPH20, SIA indicated that the top predators (i.e., fathead minnows or northern pike) occupied similar trophic levels in their respective food webs, regardless of species, size, morphology and known trophic ecology. Fatheads and pike occupied the same trophic level in SCL20, SPH200, and LLB20 probably because both fatheads and pike consumed invertebrates and young of their own species. However, trophic roles of pike and fatheads in their respective food webs differed because of the invertebrate taxa they consumed. For SPH200 and LLB20, SIA and SCA indicated that diets of pike were composed of invertebrates such as odonates and amphipods and small pike. In SCL20, based on SIA and SCA, fathead minnows also appeared to cannibalize and the invertebrates they consumed included nematodes, chironomids and various zooplankton. Detritus was also a frequent diet item for fatheads. Therefore, based on SIA and SCA, although the fathead minnows and northern pike occupied similar trophic levels, not surprisingly, their diets were different.

Fish species in SPH20 (lake that contained pike, perch, and sucker) were at a higher trophic level than similar fish species in the other study lakes. $\delta^{15}N$ values of pike and perch were 4-5 ‰ higher than those of the same species in other lakes. Pike occupied a higher trophic level likely due to the presence of white sucker in SPH20.

SPH20 was the only study lake with a third fish species present. SIA suggested that white suckers were a potential food source for the pike, although no white suckers were found in the pike stomachs. However, only a small percentage of pike stomachs collected were full and analyzed for SCA. In addition, SIA suggested that small pike and invertebrates were also potential food sources for large pike. SCA supported these findings, showing that invertebrates were the most frequent prey in fish stomachs, along with a few pike and unidentified fish, which was perhaps white sucker. Therefore, the presence of an additional prey fish species was translated into the higher trophic levels of pike in the food web.

In all the study lakes, the expected 3.4 ‰ enrichment in ^{15}N per trophic level was sometimes not observed between consumers (both fish and invertebrates) and their potential prey. Omnivory can explain a decrease in the expected 3.4 ‰ ^{15}N enrichment (Kling et al. 1992). These results add support to studies elsewhere that have shown that omnivory is common in aquatic communities (Sprules and Bowermann 1988, Vadas 1990, Kling et al. 1992, Hecky and Hesslein 1995, Diehl 1992).

Variability in isotopic signatures among fish, invertebrates, and primary producers in each lake was noted both at any one time period and throughout the summer. For fish, variability among individuals can be explained by ontogenetic diet shifts, which have been documented for both pike and perch (Hunt and Carbine 1951, Frost 1954, Lawler 1965, Clady 1973, Wu and Culver 1992). Variation can also be due to a species having a general diet, as seen in tui chubs (Estep and Vigg 1985). Despite this variability, mean isotopic signatures for each size-class of the fish species were fairly consistent over time. Little variability in the mean isotopic signatures was probably due to the low rate of tissue turnover in slow growing fish muscle tissue (Hesslein et al. 1993).

Various invertebrate taxa were not always represented in my samples perhaps due to their life cycles, or a less intensive sampling regime. Differences in the ranges of invertebrate isotopic signatures within a lake may be caused by different numbers of taxa. Nevertheless, trophic relationships, as indicated by SIA, did not appear to be altered within lakes over the summer. Although $\delta^{13}C$ signatures of some taxa did change slightly from month-to-month, shifts in $\delta^{15}N$ signatures of fish and invertebrate taxa were

generally relatively minor over the summer. Assuming a 3.4 ‰ enrichment in $\delta^{15}N$ of organisms relative to their prey (Minagawa and Wada 1984), consumers generally remained at similar trophic levels over time even if their diets changed slightly. When there were large detectable differences, changes were probably due to a shift in species or a change in developmental stages of invertebrates. Slight shifts in isotopic compositions of some taxa may have been due to diet shifts or within organism variation. Alternatively, changes in the isotopic signatures of the consumers may simply have reflected temporal changes in the isotopic signatures of their prey items, as many of the primary producers often had variable isotopic signatures throughout the summer.

A number of factors can cause the isotopic signatures of submersed macrophytes and phytoplankton to be highly variable. First, there are two main carbon sources for aquatic plants: HCO_3 and CO_2 (Lazerte and Szalados 1982). HCO_3 is -7 to -11 per mil less negative than CO_2, and the two sources may be used to different degrees, depending on the plant species and the ratio of CO_2 to HCO_3 in lakes, which, in turn, can vary diurnally and seasonally (Keeley and Sandquist 1992). Secondly, the photosynthetic pathway (C_3, C_4, or CAM) of the aquatic plants should affect their $\delta^{13}C$ signatures, as in terrestrial plants. However, isotope ratios do not always distinguish aquatic C_3, C_4 and CAM plants (Keeley and Sandquist 1992). Diffusional resistances in water, which are orders of magnitude greater than in the aerial environment, can cause variation in the $\delta^{13}C$ signature of a plant (LaZerte and Szalados 1982). Also, the greater viscosity of water acts to reduce mixing of the carbon pool in the boundary layer with the rest of the water column (Lazerte and Szalados 1982), which can result in a less negative ^{13}C:^{12}C ratio due to an accumulation of ^{13}C in the boundary layer (Keeley and Sandquist 1992). These same factors can also affect the $\delta^{13}C$ signatures of phytoplankton, as can species composition and algal growth rate (Gu et al. 1996). The $\delta^{15}N$ signatures of aquatic plants (both macrophytes and phytoplankton) can also be highly variable due to a number of factors, such as species composition, growth rate, and their ability to fix N_2 (e.g., $\delta^{15}N$ of cyanophytes decreases with increasing N_2 fixation rate; Estep and Vigg 1985, Gu et al. 1996). This variability in isotopic signatures of primary producers can cause difficulty in interpreting trophic relationships of organisms at higher trophic levels.

Not only did overlap and variability in isotope ratios of primary producers in these lakes cause ambiguity in determining some trophic relationships, the source of carbon for a consumer was sometimes ambiguous due to an apparent unknown source. Based on SIA, phytoplankton was a potential food source for consumers in some lakes at certain, but not all, times. Although phytoplankton is a common food source, certain species are not always palatable among pelagic lake organisms (de Bernardi and Guissani 1990). One unknown carbon source may have been a carbonate mineral that was ingested along with food items, which would cause an enriched $\delta^{13}C$ signature. Two other plausible food sources at the base of the food web that were not sampled in this study were epipelic algae and bacteria. Top predators have been documented to depend on both planktonic and benthic algal carbon in tropical, temperate and arctic lakes (Hecky and Hesslein 1995). Bacteria of shallow freshwater lakes, along with detrital particles, can also be an important carbon source for some zooplankton (e.g., daphnids, Hessen et al. 1989, Hessen et al. 1990, Jurgens 1994). In some eutrophic lakes, the biomass ingested by zooplankton can average 5-15 % small algae, 10-20 % detritus, and 70-85 % bacteria (Mann 1988). Therefore, it follows that in my study lakes, which are both shallow and eutrophic, both bacteria and epiphytes may have often been the unknown carbon source. Good clean samples of phytoplankton and periphyton were difficult to obtain in sufficient quantities for isotopic analysis because separation from zooplankton and sediments, respectively, was difficult. As a result, in some lakes at certain sampling times I did not always have sufficient samples to investigate the signatures of epiphytes and phytoplankton. More intensive sampling of lower trophic levels and better separation of species would help decrease the overlap in isotopic signatures of organisms.

Detritus plays an important trophic role in eutrophic lake food webs (Mann 1988, Fenchel and Jorgensen 1977). Profundal detritus, usually of aquatic origin, was a potential food source for profundal organisms, such as Chironomidae, and perhaps also for pelagic organisms, such as Chaoboridae and Daphnidae. Littoral detritus, of terrestrial origin, was a potential food source for organisms such as amphipods. Although allochthonous carbon inputs to lakes are relatively more important in small or heavily forested lakes, they may still represent only 5-10 % of internal primary production

(Gasith and Hasler 1976, Hanlon 1981). In this study, terrestrial sources were potentially utilized as a carbon source in LLB20 ("pike-perch" lake) and SPH200 ("pike-only" lake) only. The importance of allochthonous carbon in these lakes may be explained by the characteristics of the lakes and their watersheds. First, both lakes have relatively short water residence times (Table 2-1), therefore, internal carbon sources may be flushed out more quickly to be replaced with external sources. High allochthonous inputs occurred in LLB20, where the Owl River backed up into the lake in 1996. In addition, there are large wetlands in the lake's watershed that also potentially contribute large amounts of allochthonous carbon to the lake. The overall importance of detritus in these lake food webs could not be assessed quantitatively, but the origin of the detritus clearly depended on the lake, and on where the detritus was found in the lake.

Internal carbon sources used by consumers included not only phytoplankton and epiphytes, but macrophytes as well. Macrophytes represented a large component of the primary producer biomass in these boreal lakes, and are a potential carbon source for consumers. For a long time, macrophytes were ignored as a food source in freshwater ecosystems or, if they were considered, it was only as detritus (Hutchinson 1975, Polunin 1984). However, macrophytes can be a food source for certain invertebrates (Lodge 1991, Newman 1991). In my study lakes, SIA indicated that *Scirpus* sp., *Nuphar* sp., *Sagittaria* sp., *Polygonum* sp., and *Lemna* sp. were potential food sources for consumers, along with POM, phytoplankton, epiphytes, and detritus.

So, multiple primary producers may be utilized by consumers, which is reflected in the overlapping signatures of many invertebrates. Variation in isotopic composition of primary producers is often averaged out in consumers (Kiriluk et al. 1995), making it difficult to determine which primary producers were carbon sources for particular consumers. This is especially difficult when there is more than two sources of primary production (as in these lakes). Because of the number of primary producers, a two-source mixing-model to quantitatively determine the relative importance of carbon sources was inappropriate (Gearing 1991, Rosenfeld and Roff 1992).

However, there was an indication that food chains relying on distinct carbon sources existed within some food webs, as seen when there was a differentiation between

pelagic and littoral invertebrates in SPH200 and SPH20. Differentiation between the carbon isotopic signatures of pelagic and littoral organisms due to a respective dependence on phytoplankton and periphyton has been documented previously (France 1995). Still, this distinction was not as apparent in my study lakes as elsewhere, perhaps due to many of the aforementioned factors. In particular, shallow depths probably resulted in a lack of clear distinction between pelagic and littoral zones in some study lakes.

In conclusion, based on SIA and SCA, (1) two ecologically distinct fish species (i.e., fathead minnows and northern pike) occupied the same trophic level in various lakes (Fig. 2-8); (2) however, in SPH20, the lake with northern pike, yellow perch and white sucker, pike occupied a higher trophic level, perhaps due to the presence of additional prey fish (Fig. 2-8); (3) omnivory was prevalent in both invertebrates and fish; (4) trophic levels of consumers remained fairly constant over the summer even if their diets shifted slightly; and (5) internal carbon inputs appeared to be at the base of the food webs in lakes with long water residence times, whereas external inputs were important in lakes with short water residence times (Fig. 2-9).

Based on the above conclusions, the following predictions regarding the impacts of logging on food webs of lakes in Alberta's boreal forest are defensible. First, in lakes with shorter water residence times, where the use of allochthonous carbon was detectable, there may be a shift to more autochthonous carbon after logging. Heavily forested streams, which are usually allochthonous based, become more autochthonous-based after logging (Rounick et al. 1982). This switch to autotrophy in logged streams was a result of increases in algal biomass and changes in species composition due to increases in phosphorus concentration and insolation (Holopainen et al. 1991). In lakes that rely primarily on autochthonous carbon sources, an increase in internal primary productivity may result in a shift in phytoplankton species. Alternatively, if increases in primary productivity or suspended solids decrease light attenuation, heterotrophs may increase in numbers. In either case, there may not be a large impact on consumers feeding habits because most consumers in these lakes appear to be omnivores and generalists. However, specialist feeders may be at a disadvantage.

Additionally, the trophic relationships in these lakes will likely change significantly if timber harvesting results in dissolved oxygen depletion and fish kills. If dissolved oxygen concentrations in winter fall to <1-2 mg/L, fishkills may occur (Tonn and Magnuson 1982), particularly for large-bodied fish, because they are more susceptible to hypoxic conditions than smaller-bodied fish (Casselman and Harvey 1975, Tonn and Magnuson 1982). Models to predict winter oxygen depletion rates (WODR) have been developed by several investigators (Welch et al. 1976, Barica and Mathias 1979, Babin and Prepas 1985). The model developed by Babin and Prepas (1985) predicts WODR in a large range of lake types, including highly productive lakes of north-central Alberta. A combination of mean summer total phosphorus (TP_{su} in mg/m^2) in the euphotic zone and mean depth ($\bar{z}$ in m) was used to develop the following equation:

$$WODR = -0.101 + 0.00247*TP_{su} + 0.0134*\bar{z}$$

Assuming 100% saturation of oxygen in the lakewater just prior to lake ice formation, it is likely that hypoxic conditions could have occurred in LLB20 and LLB800 during 1995 and 1996 based on the Babin and Prepas (1985) WODR model. The shallow depth of LLB20 can explain the lake's susceptibility to hypoxia, whereas the susceptibility of LLB800 can be explained by its eutrophic trophic status. In 1996, a severe winterkill occurred in LLB800, but the role of logging in the watershed two years earlier is unknown and is under investigation by others. However, if SCL20, SPH20 and SPH200 are not 100% saturated when ice forms, it is likely that they too could become hypoxic over winter. These predictions assume a lack of oxygenated areas due to springs in the lakes, which may serve as refuges for fish. Also, snow cover and excessive ice, two factors that contribute to winter hypoxia (Barica et al. 1983), are not incorporated into the model.

If fish populations are decimated by low dissolved oxygen concentrations, an alteration in food web structure will likely occur (Tonn and Paszkowski 1986). The impact of a loss of a fish species on the food web will depend on the role that species plays in the food web. Although pike and fatheads occupied the same trophic level regardless of their sizes and morphologies, the diets of the fish species differed. Small-bodied fatheads are less likely to experience a winterkill (Casselman and Harvey 1975),

but if they were decimated, their prey (e.g., nematodes, chironomids, and various zooplankton) may increase in numbers due to reduced predation pressure. If a fishkill occurred in the "pike-only" lake, invertebrates such as odonates and amphipods could increase in numbers, which in turn, could result in decreased numbers of invertebrates at lower trophic levels. In both lakes that contained pike as well as other fish species, all fish species may be eliminated due to hypoxic conditions as in LLB800, resulting in increased diversity and abundance of invertebrates. The relationship between drainage basin disturbance and fish assemblages in lakes is an important aspect of renewable resource management that deserves further attention.

Table 2-1: Physical, chemical, and biological parameters of the five study lakes, LLB800, SCL20, SPH200, LLB20 and SPH20,during summer 1996 (fish species: fathead minnow (fh), northern pike (np), yellow perch (yp), white sucker (ws), and brook stickleback (bs)).

Lake	Fish assemblage	Fish species	Location (N,W)	Bottom depth z_{max} (z_{mean}) (m)	Water residence times* (y)	mean summer pH	mean summer*** total phosphorus (µg/L)
LLB800	"fishless"		55°12', 111°38'	6.8 (3.0)	4	7.3	58+/-7
SCL20	"fathead"	fh	55°11', 113°39'	11.2 (4.9)	2	8.4	48+/-6
SPH200	"pike-only"	np, bs**	55°23', 113°38'	9.5 (4.1)	1	7.8	40+/-5
LLB20	"pike-perch"	np, yp	55°8', 111°45'	5.8 (2.1)	<<1	7.5	47+/-5
SPH20	"pike-other"	np, yp, ws	55°25', 113°42'	8.5 (4.4)	2	7.5	22+/-1

* estimate with ground water flow (Appendix I) ** only a few individuals caught in the month of June 1996

***mean summer total phosphorus for each lake was calculated with June, July and August values

Table 2-2: Symbols for all figures in Chapter 2. Please note: Abbreviations of large and small fish are in uppercase and lowercase letters, respectively; littoral invertebrates are in lowercase letters; pelagic invertebrates are in uppercase letters.

Organism	Symbol	Organism	Symbol
Invertebrates		**Fish**	
Odonata		*Esox lucius* >85mm	NP
Anisoptera larvae	an	*Esox lucius* ≤85mm	np
Zygoptera larvae	zy	*Perca flavescens* >150mm	YP
Hemiptera		*Perca flavescens* ≤150mm	yp
Notonectidae	not	*Catostomus commersoni*	WS
Corixidae	co/CO	*Culaea inconstans*	BS
Coleoptera	col	*Pimephales promelas*	FH
Coleoptera larvae	lco	**Macrophytes**	
Chrysomelidae	chr	emergent	
Dytiscidae	dy	*Equisetum* sp.	eq
Gyrinidae	gy	*Scirpus* sp.	sc
Hydrophilidae	hy	*Typha* sp.	ty
Hirudinea	hir	rushes	ru
Erpobdellidae	er	floating	
Glossiphonidae	gl	*Lemna* sp.	le
Ephemeroptera		*Nuphar* sp.	nu
Caenidae larvae	cae	*Polygonum* sp.	po
Trichoptera	tri	*Sagittaria* sp.	sa
Glossosomatidae larvae	glo	submergent	
Limnephilidae larvae	li	*Alisma* sp.	al
Molannidae larvae	mo	*Ceratophyllum* sp.	ce
Phryganeidae larvae	phr	*Myriophyllum* sp.	my
Rhyacophilidae larvae	rhy	*Potamogeton* sp.	pot
Gastropoda	gas	**Other primary producers**	
Lymnaeidea	lym	*Chaetophora* sp.	c
Physidae	phy	*Chara* sp.	ch
Planorbidae	pla	*Cladophora* sp.	cla
Crustacea		*Gloeotrichia* sp.	gloe
Amphipoda	am/AM	*Nostoc* sp.	nos
Daphnidae	DA	*Rhizoclonium* sp.	rhi
Copepoda	COP	epiphytes	epi
Other families		mosses	moss
pooled zooplankton	ZO	phytoplankton	P
Hydracarina	mi/MI	particulate organic matter	POM
Chaoboridae larvae	CHA	terrestrial leaves or humus	t
Chironomidae larvae	chi/CHI	**Detritus**	
Oligochaetae	ol	profundal	pd
Tadpoles	tad	littoral	ld

Table 2-3: Frequency of occurrence of prey taxa consumed by fish species in SCL20, SPH200, LLB20, and SPH20 during summer 1996 (np (northern pike), yp (yellow perch), ws (white sucker) and fh (fathead minnow)).

Prey Item	SCL20	SPH200		LLB20
	fh (n=47)	np>85mm (n=38)	np≤85mm (n=7)	np>85mm (n=12)
Macroinvertebrates				
Amphipoda	0.1	0.7	0.8	0.4
Odonata larvae	0.1			
Anisoptera larvae		0.5		0.2
Zygoptera larvae	0.02	0.4		
Chironomidae larvae	0.4		0.3	0.1
Coleoptera larvae	0.04			
Diptera				
Gastropoda				
Hirudinea				
Nematoda	0.3			
Notonectidae				
Pelycepoda				
Trichoptera larvae	0.02	0.1		
unidentified invertebrate	0.3	0.1		0.1
terrestrial invertebrate	0.2			
Zooplankton				
Bosminidae	0.1			
Chaoboridae larvae	0.02	0.03	0.3	
Cladocera	0.4			
Copepoda	0.02			
Hydrachnidia	0.03			
Rotifera	0.1	0.03		
unidentified zooplankton	0.1			
Fish				
P. flavescens				0.1
E. lucius		0.1		0.3
C. inconstans		0.1		
unidentified fish				0.2
fish scales	0.2			0.1
fin part	0.2			
Other				
filamentous algae	0.03		0.1	
other phytoplankton	0.1			
macrophytes		0.1		0.2
bryophytes	0.02			
Nostoc sp.				
detritus	0.9	0.1	0.5	0.2
seeds	0.5			
Picea sp. needles				

Table 2-3: (continued)

Prey Item	LLB20		SPH20		
	yp>150mm (n=15)	yp≤150mm (n=6)	np>85mm (n=13)	yp≤150mm (n=12)	ws>400mm (n=2)
Macroinvertebrates					
Amphipoda	0.7	0.8	0.1	0.8	
Odonata larvae					
Anisoptera larvae	0.1		0.3		
Zygoptera larvae	0.1				
Chironomidae larvae	0.4	0.3	0.1	0.4	
Coleoptera larvae	0.1	0.2	0.1	0.2	
Diptera			0.1		
Gastropoda			0.1		
Hirudinea			0.1		
Nematoda				0.1	
Notonectidae	0.2			0.1	
Pelycepoda	0.1		0.1		
Trichoptera larvae			0.1		
unidentified invertebrate	0.1			0.1	
terrestrial invertebrate					
Zooplankton					
Bosminidae					
Chaoboridae larvae	0.1			0.8	
Cladocera		0.2		0.3	
Copepoda		0.2			
Hydrachnidia					
Rotifera					
unidentified zooplankton					
Fish					
P. flavescens			0.2		
E. lucius			0.1		
C. inconstans					
unidentified fish			0.1		
fish scales	0.1				
fin part		0.2			
Other					
filamentous algae	0.1	0.2			
other phytoplankton					
macrophytes	0.3	0.2			
bryophytes					
Nostoc sp.			0.1		
detritus	0.2		0.1		1.0
seeds					
Picea sp. needles			0.2		

Table 2-4: Means(+/-SE) of $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of fish species in SCL20, SPH200, LLB20, and SPH20 during summer 1996.

Lake	Fish species and Size-class	Sample size (n)	$\delta^{13}C$ mean+/-SE	$\delta^{15}N$ mean+/-SE
SCL20	*P. promelas*	44	-26.6 +/- 0.2	13.6 +/- 0.1
SPH200	*E. lucius* >85 mm	28	-26.9 +/- 0.3	11.4 +/- 0.3
	E. lucius ≤85 mm	5	-27.1+/- 0.4	9.2 +/- 0.2
	C. inconstans	4	-29.9 +/- 0.2	11.5 +/- 0.1
LLB20	*E. lucius* >85 mm	18	-27.0 +/- 0.5	12.4 +/- 0.4
	P. flavescens >150 mm	6	-27.2+/-0.2	11.2+/-0.3
	P. flavescens ≤150 mm	11	-28.7+/-0.4	12.8+/-0.4
SPH20	*E. lucius* >85 mm	14	-25.4 +/- 0.3	17.1 +/- 0.1
	P. flavescens ≤150 mm	12	-28.1 +/- 0.1	16.7 +/- 0.2
	C. commersoni	2	-26.1 +/- 1.2	14.8 +/- 1.1

Table 2-5: Means(+/-SE) and ranges of $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of fish species over time in SPH200 and SCL20 during summer 1996.

Month	Lake	Fish species and size-class	Sample size (n)	δ^{13} C		δ^{15} N	
				mean+/-SE	range	mean+/-SE	range
May	SPH200	*E. lucius* >85mm	1	-27.5	na	12.2	na
June		*E. lucius* >85mm	6	-27.2+/-0.3	2.13	11.8+/-0.5	3
		E. lucius ≤85mm	5	-27.1+/-0.4	2.26	9.2+/-0.2	0.9
		C. inconstans	4	-29.9+/-0.2	1.04	11.5+/-0.1	0.5
August		*E. lucius* >85mm	22	-26.8+/-0.3	4.83	11.2+/-0.3	4.6
May	SCL20	*P. promelas*	5	-28.1+/-0.2	1.15	13.8+/-0.2	1.3
June		*P. promelas*	5	-29.3+/-0.3	1.78	14.5+/-0.4	2.2
August		*P. promelas*	30	-25.9+/-0.2	3.82	13.5+/-0.1	2.3
September		*P. promelas*	4	-26.9+/-0.1	0.39	13.7+/-0.3	1

Table 2-6: Means(+/-SE) and ranges of $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of individuals within invertebrate taxa collected at one sampling period (June 1996) in SPH200.

Invertebrate taxa	Sample size	δ^{13} C		δ^{15} N	
	n	mean+/-SE	range	mean+/-SE	range
Amphipoda	3	-28.0+/-0.8	2.6	4.4+/-0.4	1.3
Corixidae	3	-29.5+/-0.4	1.5	6.8+/-0.7	2.2
Notonectidae	3	-28.8+/-1.8	5.7	7.4+/-1.1	3.8
Zygoptera	3	-28.6+/-0.6	2.0	8.6+/-0.5	1.4
Anisoptera	3	-28.5+/-0.6	2.0	5.9+/-0.5	1.7
Chironomidae	3	-32.5+/-0.4	1.3	3.8+/-0.2	0.5

Table 2-7: Frequency of occurrence of prey taxa consumed by northern pike (>85 mm* and ≤85 mm**) in SPH200 and fathead minnows in SCL20 from May to August 1996.

Lake	Fish	Prey item	Months			
SPH200	Northern pike		May (n=1)*	June (n=18)*	June (n=7)**	August (n=19)*
		Invertebrates				
		Amphipoda	1.0	0.9	0.8	0.5
		Anisoptera larvae		0.7		0.4
		Chaoboridae larvae			0.3	0.1
		Chironomidae larave			0.3	
		Rotifera				0.1
		Trichoptera larvae		0.3		
		Zygoptera larvae		0.6		0.3
		unidentified invertebrate		0.1		0.1
		Fishes				
		Northern pike		0.2		0.1
		Brook stickleback				0.2
		Other				
		filamentous algae			0.1	
		macrophytes				0.2
		detritus			0.5	0.1
SCL20	Fathead minnow		May (n=11)	June (n=12)	August (n=16)	September (n=8)
		Invertebrates				
		Amphipoda	0.2	0.2	1.0	
		Chaoboridae larvae		0.1		
		Chironomidae larvae	0.1	0.6	0.6	
		Cladocera	0.1	0.4	0.6	0.3
		Coleoptera		0.2		
		Copepoda			0.1	
		Hydrachnidia		0.1	0.2	
		Nematoda	0.6	0.2	0.1	0.1
		Rotifera			0.2	
		Trichoptera larvae		0.1		
		unidentified invertebrate	0.3	0.5	0.3	
		Zygoptera		0.1		
		Other				
		detritus	1.0	1.0	0.8	1.0
		seeds	0.7	0.6	0.2	0.8
		fin part	0.3	0.3	0.1	0.1
		fish scales	0.3	0.3	0.3	
		algae	0.3			
		filamentous algae	0.1			
		moss		0.1		

Table 2-8: Means(+/-SE) and ranges of $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of invertebrates from all sampling times in SCL20, SPH200 and LLB800 during summer 1996.

Lake	Organism	Sample size (n)	δ^{13} C mean+/-SE	δ^{13} C range	δ^{15} N mean+/-SE	δ^{15} N range
SCL20	**Littoral**					
	Chironomidae larvae	3	-28.2+/-1.2	4.2	10.8+/-0.3	0.8
	Corixidae	4	-26.0+/-0.3	1.3	6.7+/-0.8	3.3
	Erpobdellidae	4	-27.5+/-0.7	3.2	10.6+/-0.3	1.5
	Amphipoda	4	-26.6+/-0.1	2.4	6.7+/-0.1	0.5
	Glossiphonidae	3	-26.0+/-1.0	3.6	11.3+/-0.7	2.3
	Molannidae larvae	3	-27.9+/-0.4	1.4	10.2+/-0.6	2.1
	Phryganeidae larvae	4	-26.4+/-1.7	8.1	8.9+/-0.4	1.9
	Pelagic					
	Chaoboridae larvae	3	-27.9+/-0.9	3.2	11.6+/-1.1	3.8
	Hydrachnidia	3	-28.8+/-1.2	4.0	12.1+/-0.3	1.0
	zooplankton >243µ	4	-29.6+/-0.8	3.4	10.1+/-0.6	2.7
SPH200	**Littoral**					
	Anisoptera larvae	4	-27.4+/-1.3	5.6	7.3+/-0.3	1.6
	Dytiscidae	3	-28.4+/-0.6	1.9	7.1+/-0.4	1.2
	Notonectidae	4	-29.6+/-0.7	3	8.0+/-0.7	3.4
	Zygoptera larvae	4	-27.0+/-0.6	2.6	7.7+/-0.8	3.8
	Corixidae	4	-28.2+/-0.7	3.2	5.8+/-0.8	3.1
	Chironomidae larvae	3	-27.3+/-2.6	8.3	6.0+/-0.7	2.3
	Limnephilidae larvae	3	-25.2+/-1.4	4.3	5.6+/-0.5	1.5
	Amphipoda	3	-26.3+/-0.9	3.3	4.6+/-0.4	1.6
	Physidae	4	-27.3+/-0.9	4.3	5.7+/-0.4	2
	Planorbidae	4	-25.9+/-0.5	2.4	5.5+/-0.6	2.3
	Pelagic					
	Hydrachnidia	3	-28.3+/-1.3	4.2	7.9+/-0.6	2.1
LLB800	**Littoral**					
	Corixidae	4	-24.0+/-0.6	2.8	7.2+/-0.8	3.4
	Dytiscidae	4	-23.0+/-0.5	2.2	9.4+/-0.4	1.9
	Hydrophilidae	3	-24.0+/-0.5	1.7	7.1+/-1.1	3.8
	Erpobdellidae	4	-22.3+/-0.3	1.6	11.9+/-0.3	1.6
	Amphipoda	4	-23.8+/-0.6	2.8	9.1+/-0.8	3.5
	Glossiphonidae	4	-18.9+/-1.4	6.4	11.3+/-0.4	1.6
	Lymnaeidae	3	-16.7+/1.1	3.5	7.6+/-0.3	1.0
	Notonectidae	4	-24.2+/-0.5	2.2	8.0+/-0.7	3.4
	Physidae	4	-19.6+/-1.3	5.9	8.4+/-0.5	1.9
	Planorbidae	4	-18.3+/-0.7	2.8	6.7+/-0.3	1.3
	Zygoptera larvae	4	-21.7+/-0.3	1.2	11.4+/-0.5	2.3
	Pelagic					
	Chaoboridae larvae	3	-25.1+/-1.1	3.5	10.2+/-0.4	1.5
	Hydrachnidia	3	-24.2+/-0.6	2.0	10.3+/-1.0	3.5
	Chironomidae larvae	4	-26.0+/-1.1	5.3	8.9+/-0.8	3.7
	zooplankton >500µ	3	-22.6+/-0.1	0.4	6.4+/-1.1	3.8

Table 2-9: Means(+/-SE) and ranges of $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of primary producers and detritus from all sampling times in SCL20, SPH200 and LLB800 during summer 1996.

Lake	Organisms	Sample size	δ^{13} C		δ^{15} N	
		(n)	mean+/-SE	range	mean+/-SE	range
SCL20	phytoplankton 63 µ	3	-27.6+/-3.6	11.8	4.3+/-1.1	3.4
	particulate organic matter	3	-29.9+/-1.0	3.5	7.4+/-1.4	4.3
	Nuphar sp.	3	-22.0+/-3.1	9.6	4.2+/-2.0	6.1
	profundal detritus	4	-30.4+/-0.8	0.4	3.3+/-0.6	2.4
SPH200	*Ceratophyllum* sp.	3	-18.5+/-1.8	6.2	1.0+/-0.8	2.5
	Potamogeton zosteriformis	3	-13.5+/-1.1	3.7	-2.4+/-2.5	7.9
	Nuphar sp.	4	-23.9+/-0.5	2.1	0.7+/-0.8	3.5
	profundal detritus	3	-31.7+/-0.2	0.6	2.2+/-0.6	2.0
LLB800	particulate organic matter	3	-25.2+/-1.1	3.8	8.4+/-3.3	11.2
	Lemna trisulca	4	-20.4+/-2.1	9.5	7.5+/-1.2	5.2
	Nuphar sp.	3	-23.4+/-0.6	2.1	6.3+/-0.9	2.8
	Potamogeon richardsonii	3	-12.8+/-0.6	1.9	7.9+/-1.2	4
	Sagittaria sp.	3	-25.7+/-0.4	1.2	5.8+/-1.1	3.5
	littoral detritus	3	-25.4+/-0.6	1.8	3.9+/-0.7	2.3
	profundal detritus	4	-29.6+/-0.1	0.4	3.9+/-0.5	1.8

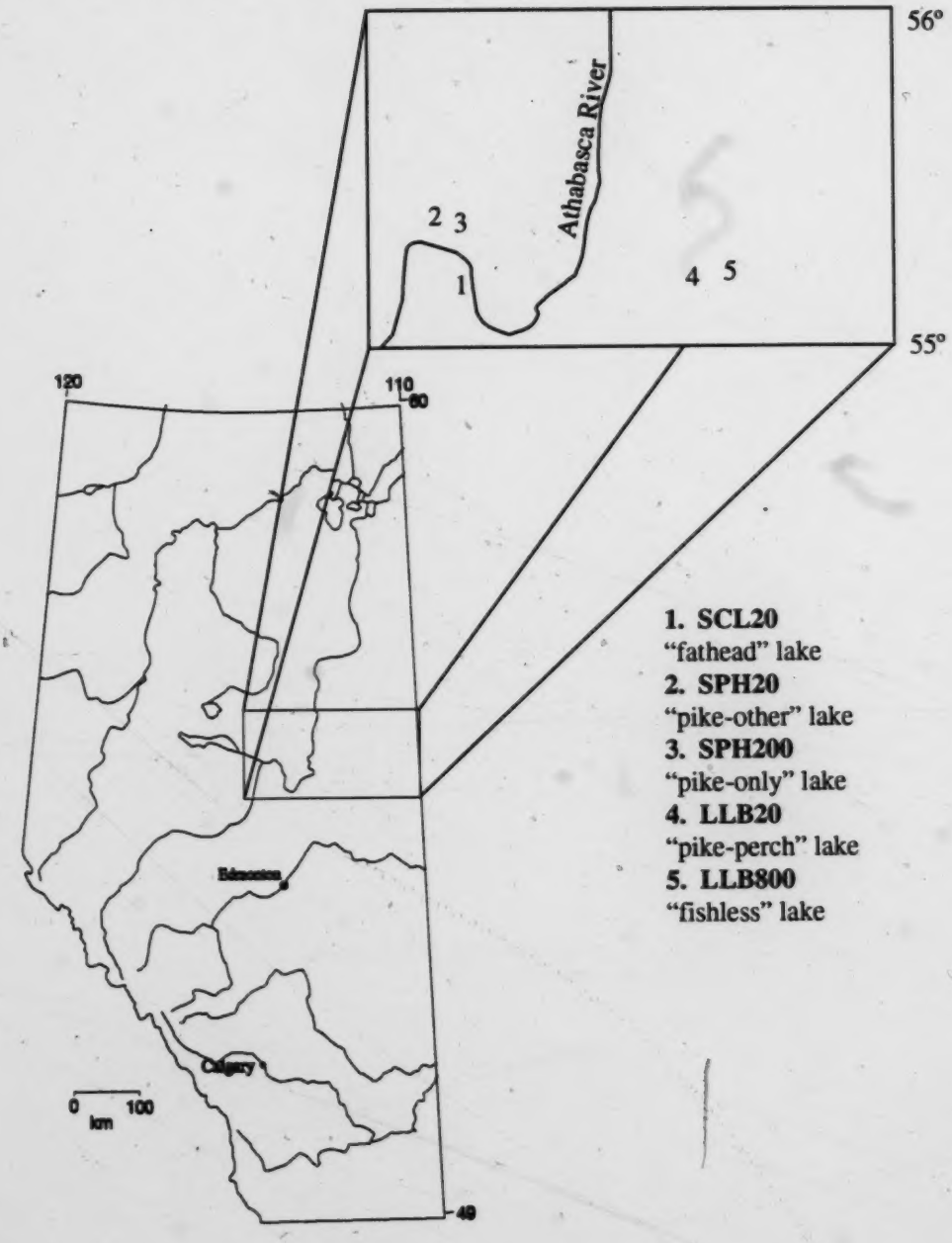

Figure 2-1: Alberta map showing the location of the study lakes.

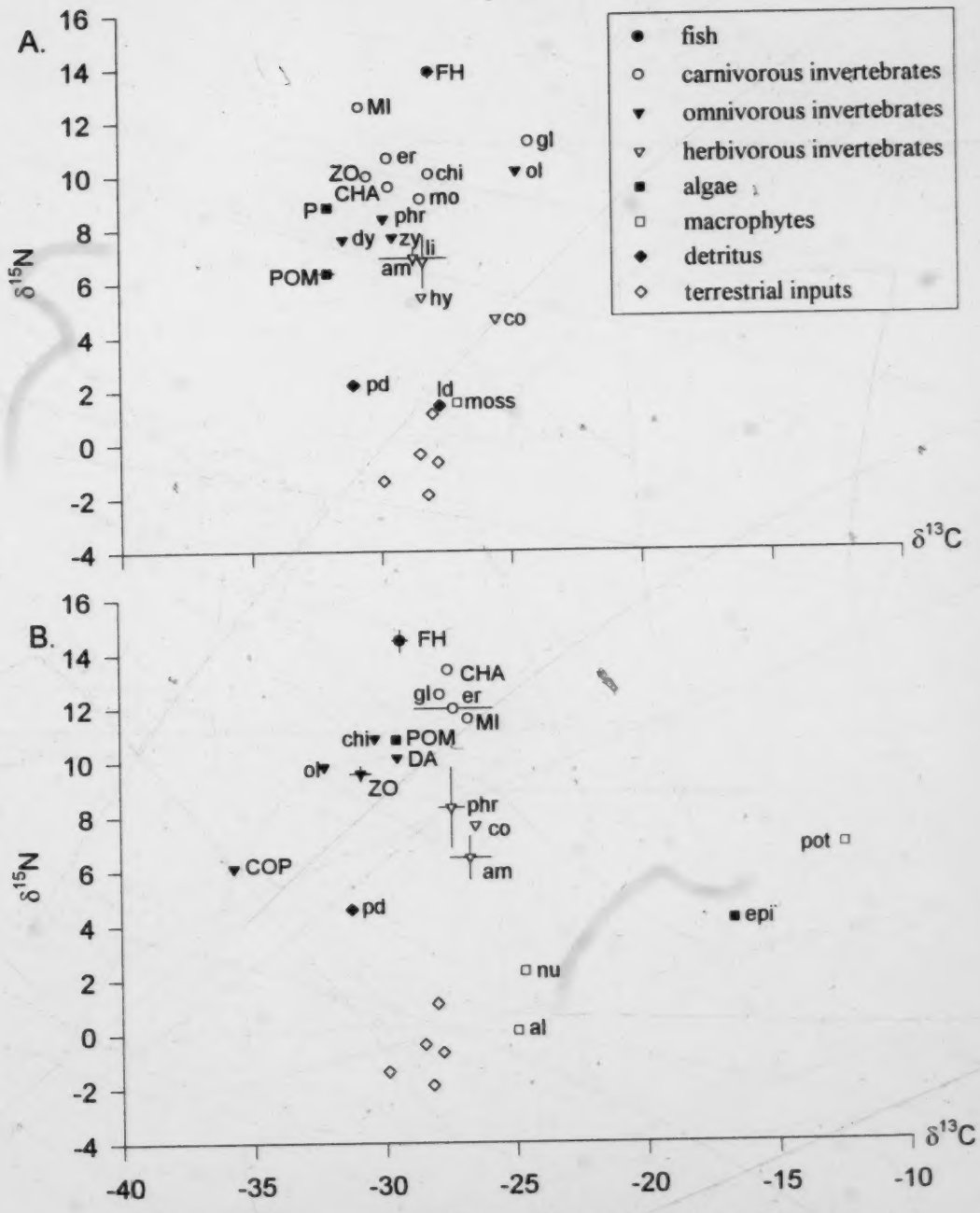

Figure 2-2: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of common taxa collected in SCL20 during May (A) and June (B) 1996. When possible, mean (+/- SE) values are plotted. Table 2-2 lists abbreviations of taxa. For fish, uppercase letters indicate large size-classes and lowercase letters indicate small size-classes; for invertebrates, uppercase letters indicate profundal and/or pelagic invertebrates and lowercase letters indicate littoral invertebrates.

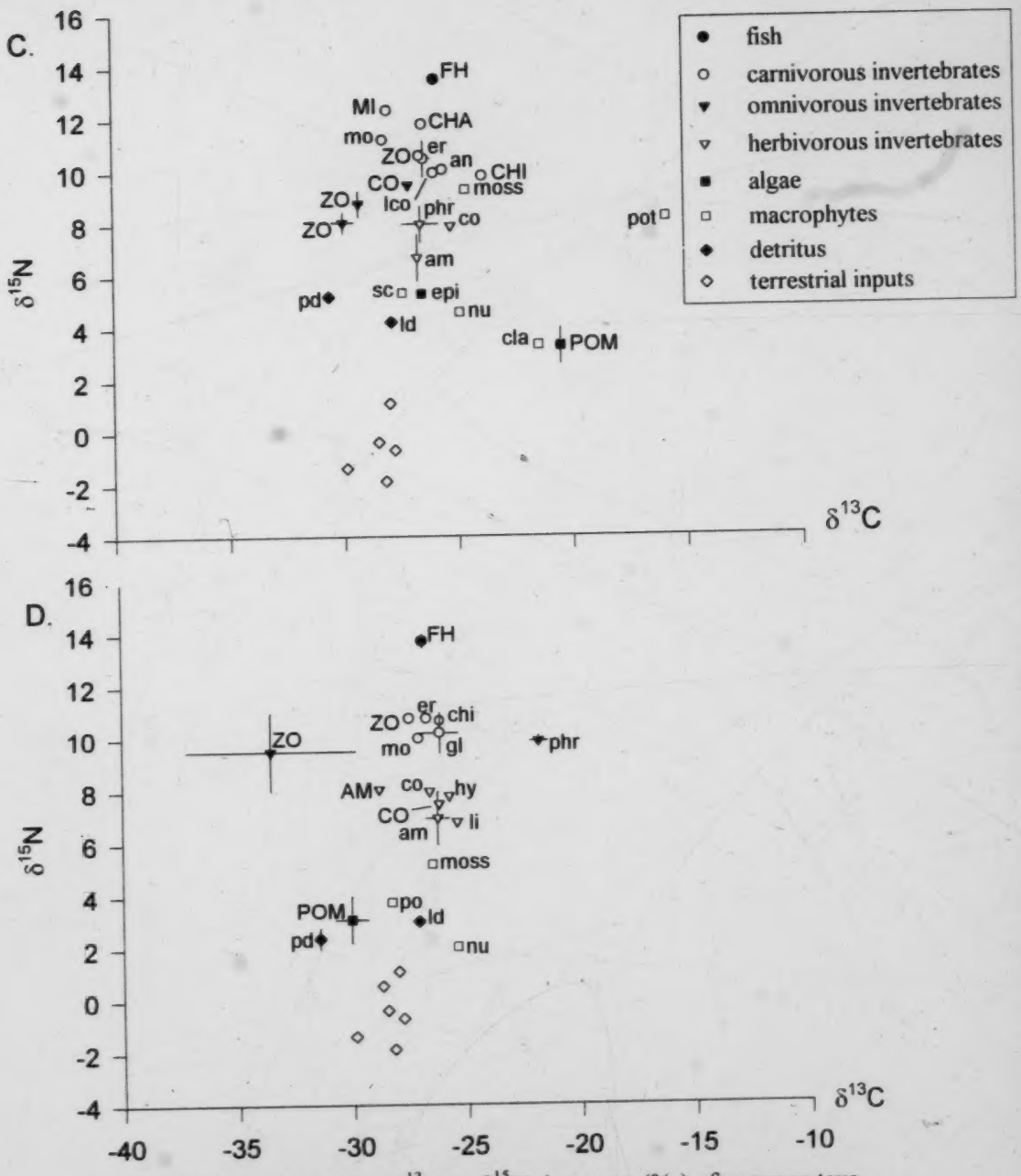

Figure 2-2: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of common taxa collected in SCL20 during August (C) and September (D) 1996. When possible, mean (+/- SE) values are plotted. Table 2-2 lists abbreviations of taxa. For fish, uppercase letters indicate large size-classes and lowercase letters indicate small size-classes; for invertebrates, uppercase letters indicate profundal and/or pelagic invertebrates and lowercase letters indicate littoral invertebrates.

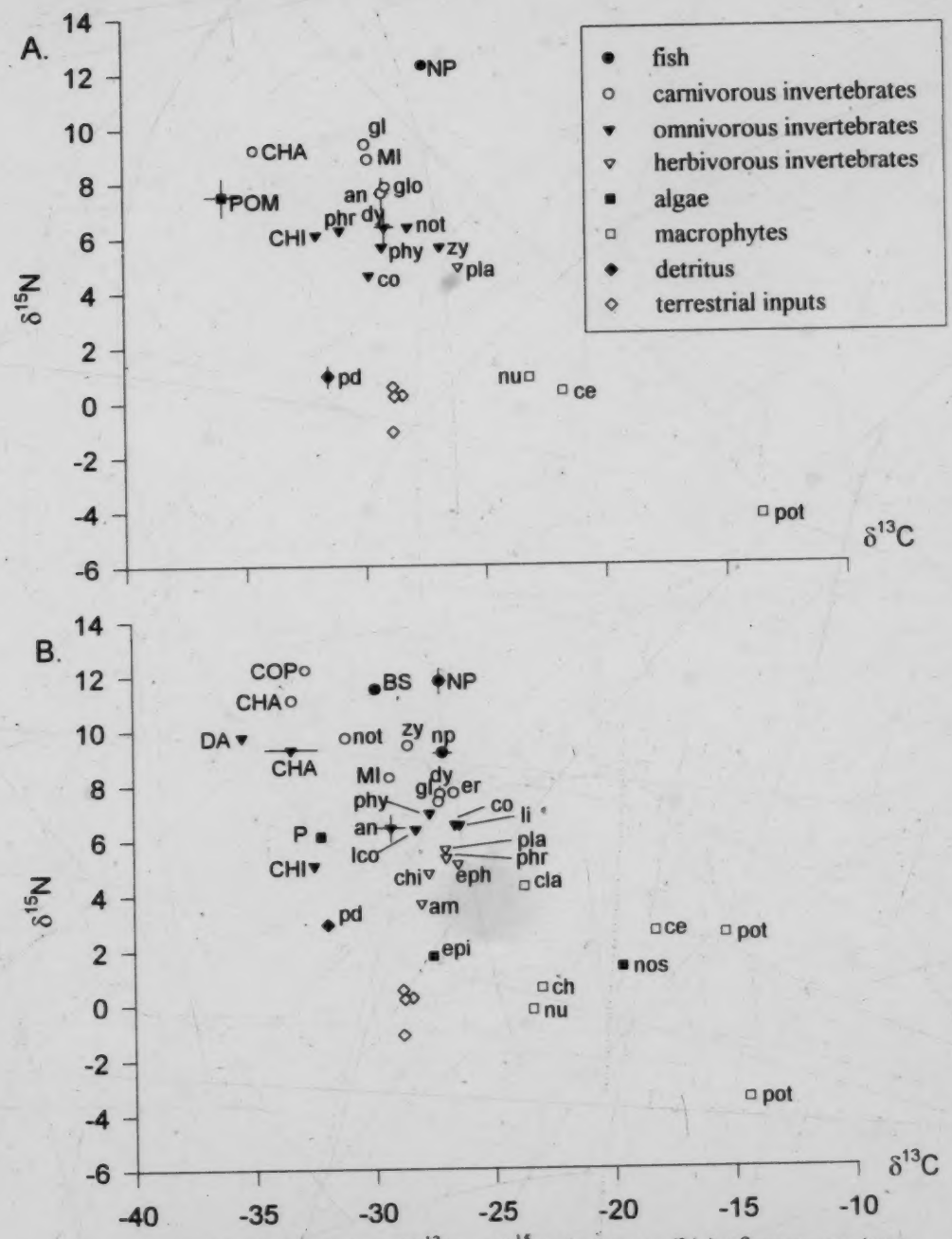

Figure 2-3: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of commone taxa collected in SPH200 during May (A) and June (B) 1996. When possible, mean (+/- SE) values are plotted. Table 2-2 lists abbreviations of lake taxa. For fish, uppercase letters indicate large size-classes and lowercase letters indicate small size-classes; for invertebrates, uppercase letters indicate profundal and/or pelagic invertebrates and lowercase letters indicate littoral invertebrates.

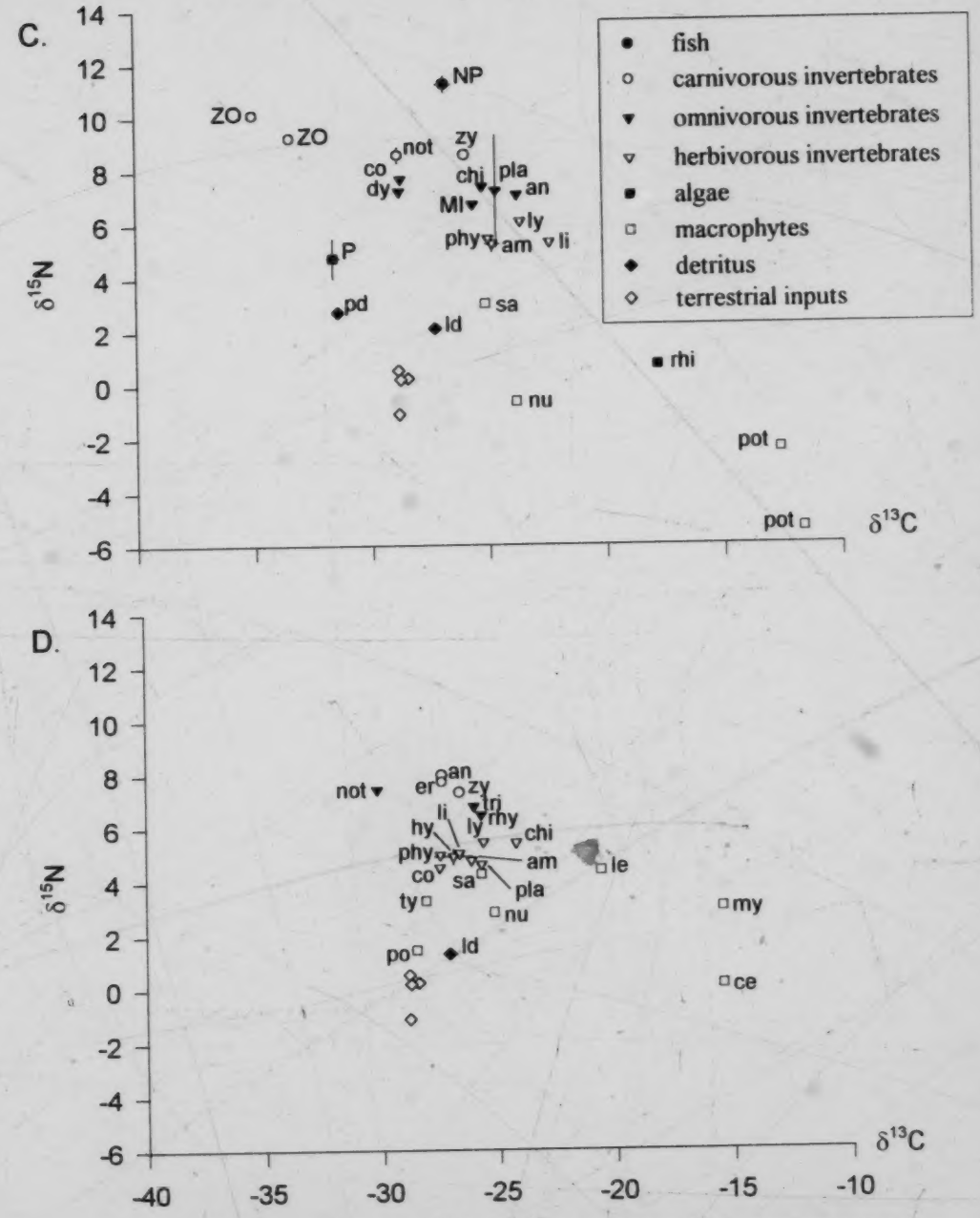

Figure 2-3: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of common taxa collected in SPH200 during August (C) and September (D) 1996. When possible, mean (+/- SE) values are plotted. Table 2-2 lists abbreviations of lake taxa. For fish, uppercase letters indicate large size-classes and lowercase letters indicate small size-classes; for invertebrates, uppercase letters indicate profundal and/or pelagic invertebrates and lowercase letters indicate littoral invertebrates.

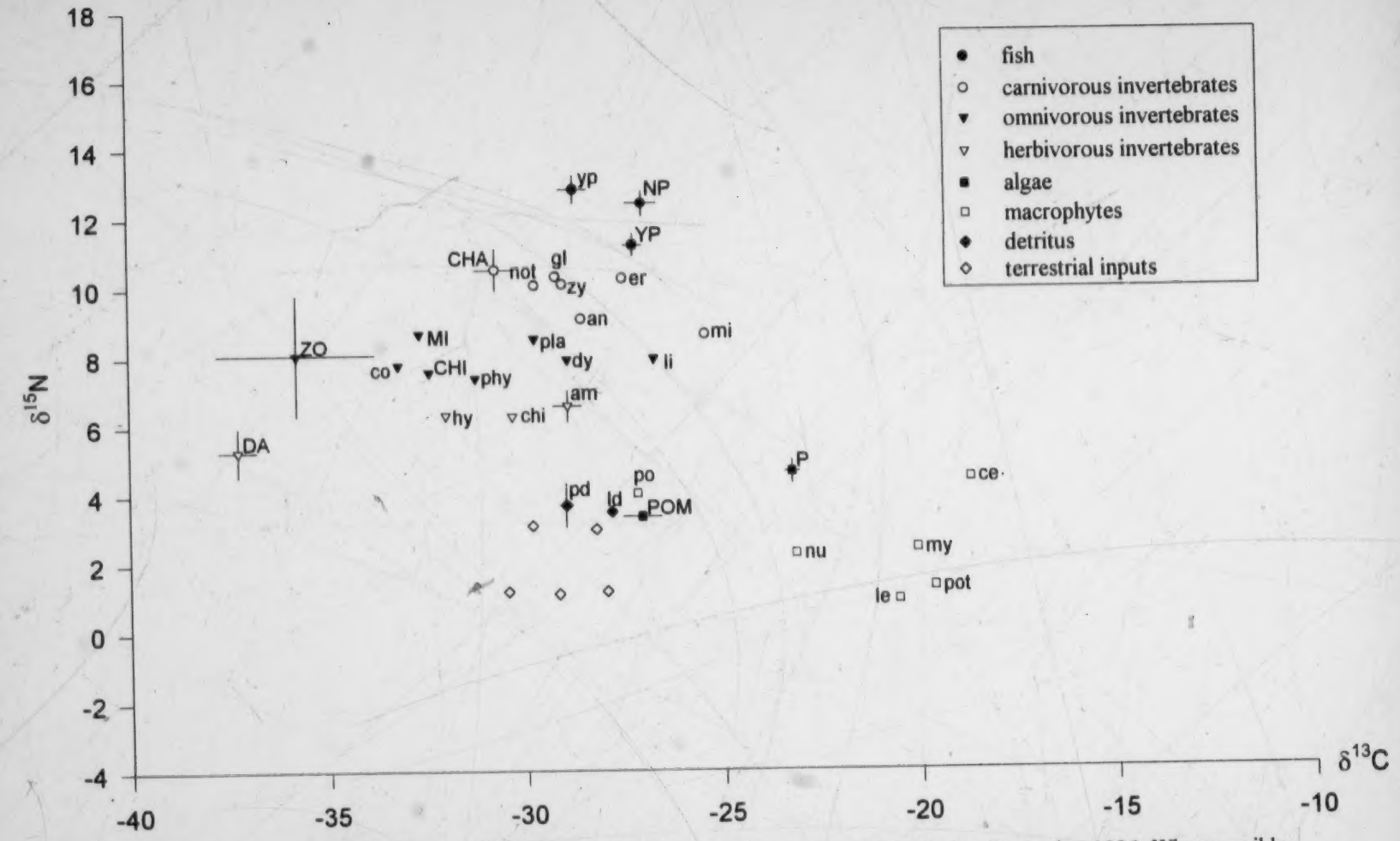

Figure 2-4: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of common taxa in LLB20 during September 1996. When possible, mean (+/- SE) values of taxa are plotted. Table 2-2 lists abbreviations of lake taxa. For fish, uppercase letters indicate large size-classes and lowercase letters indicate small size-classes; for invertebrates, uppercase letters indicate pelagic or profundal invertebrates and lowercase letters indicate littoral invertebrates.

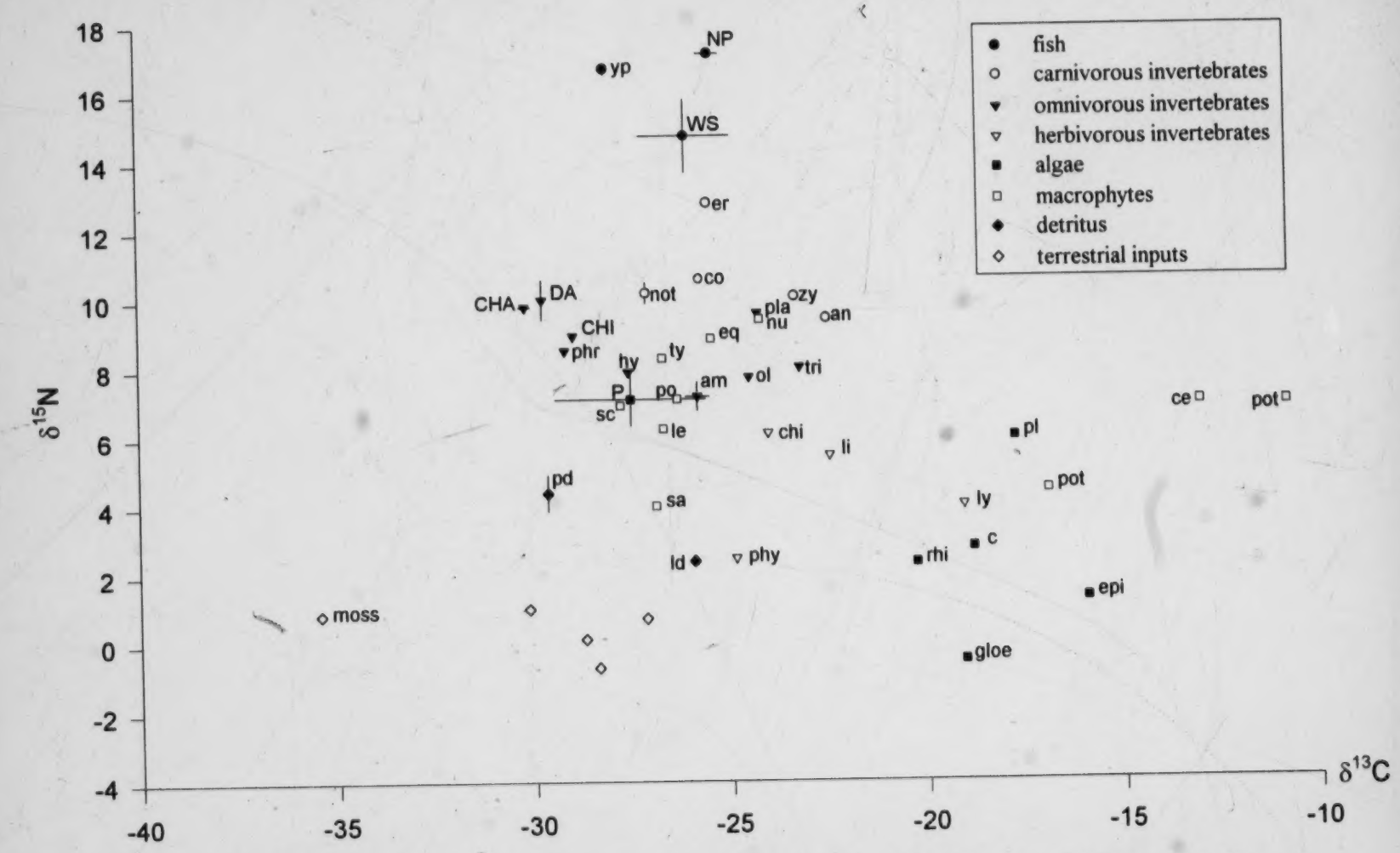

Figure 2-5: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of common taxa collected in SPH20 during August 1996. When possible, mean (+/- SE) values of taxa are plotted. Table 2-2 lists abbreviations of lake taxa. For fish, uppercase letters indicate large size-classes and lowercase letters indicate small size-classes; for invertebrates uppercase letters indicate pelagic or profundal invertebrates and lowercase letters indicate littoral invertebrates.

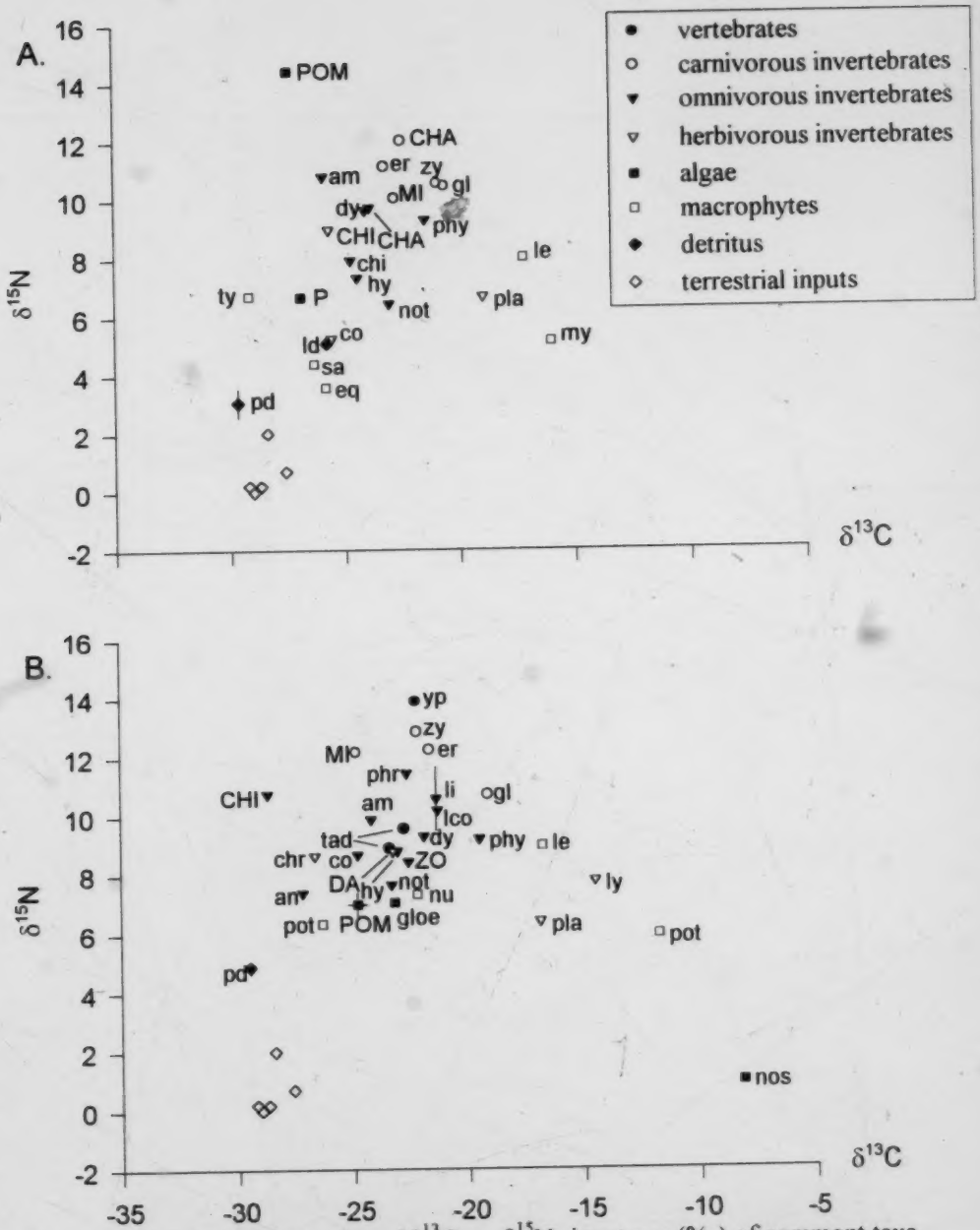

Figure 2-6: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of commont taxa collected in LLB800 during May (A) and June (B) 1996. When possible, mean (+/- SE) values are plotted. Table 2-2 lists abbreviations of taxa. For fish, uppercase letters indicate large size-classes and lowercase letters indicate small small size-classes; for invertebrates, uppercase letters indicate pelagic and/or profundal invertebrates and lowercase letters indicate littoral invertebrates.

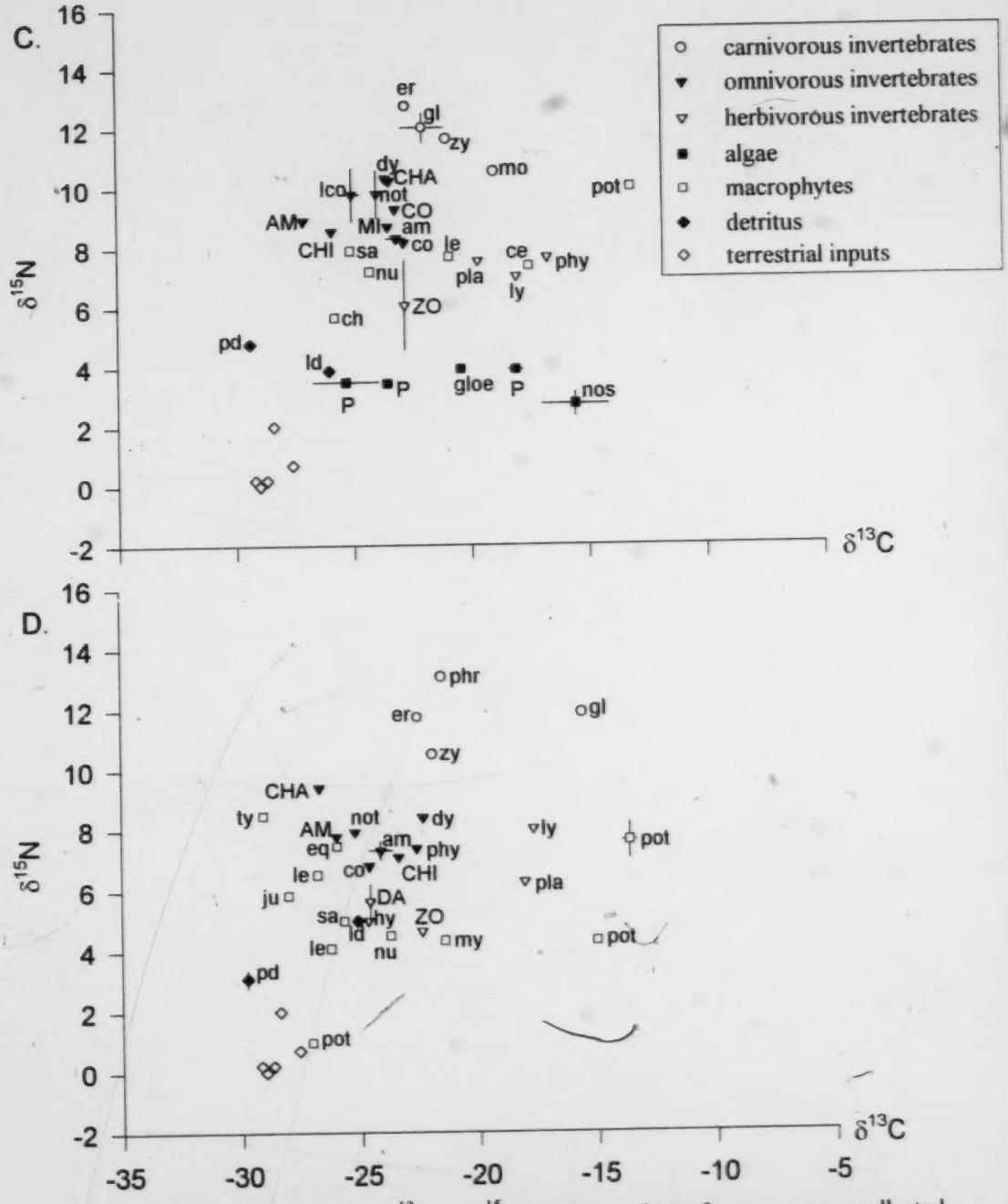

Figure 2-6: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of common taxa collected in LLB800 during August (C) and September (D) 1996. Mean (+/- SE) values are plotted when possible. Table 2-2 lists abbreviations of taxa. For fish, lowercase letters indicate small size-classes; for invertebrates, uppercase letters indicate pelagic and/or profundal invertebrates and lowercase letters indicate littoral invertebrates.

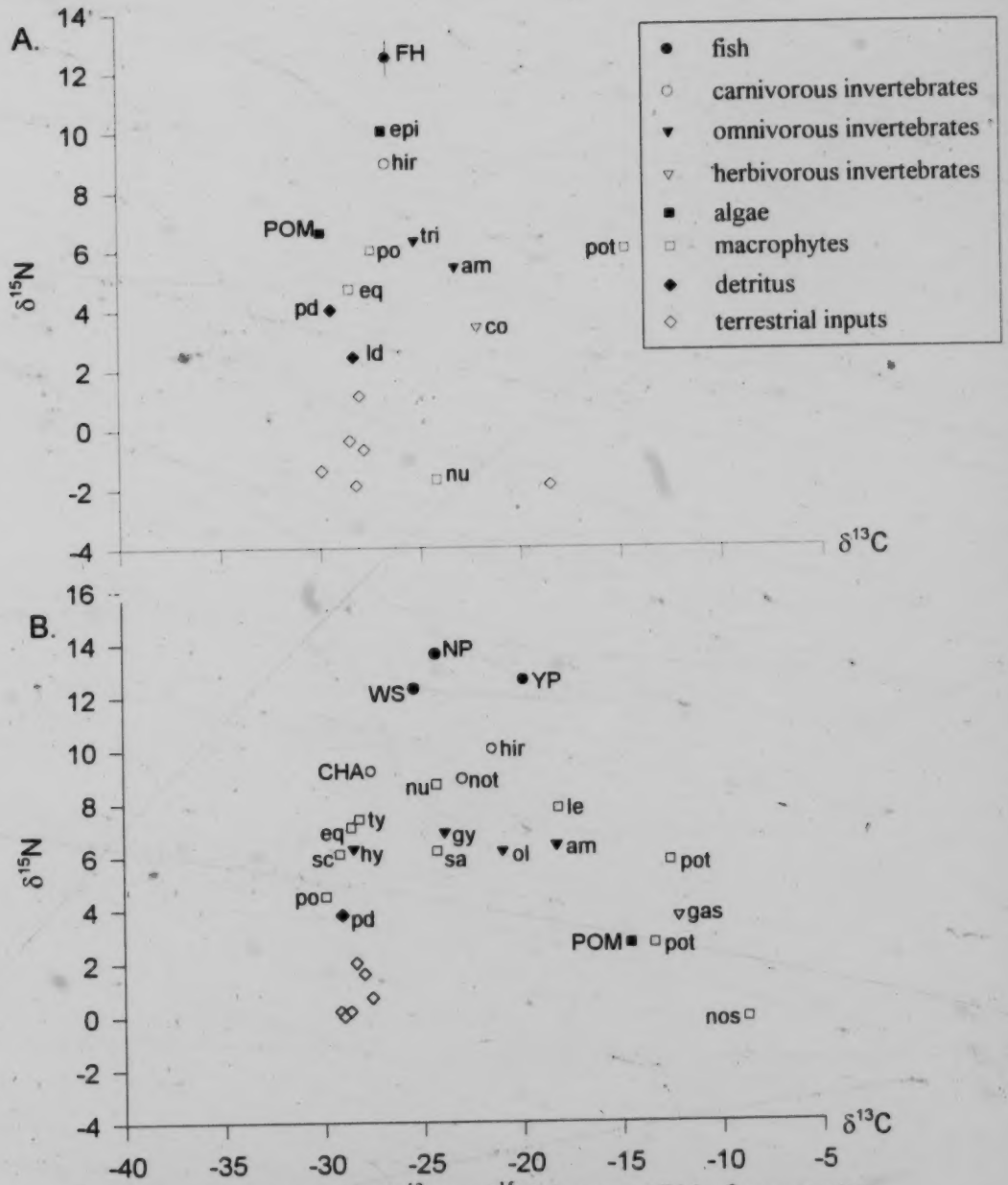

Figure 2-7: Scatter plot of $\delta^{13}C$ vs. $\delta^{15}N$ signatures (‰) of common taxa collected in SCL20 (A) and LLB800 (B) during August 1995. When possible, mean (+/- SE) values are plotted. Table 2-2 lists abbreviatiations for lake taxa. For fish, uppercase letters indicate large size-classes; for invertebrates, uppercase letters indicate profundal and/or pelagic invertebrates and lowercase letters indicate littoral invertebrates.

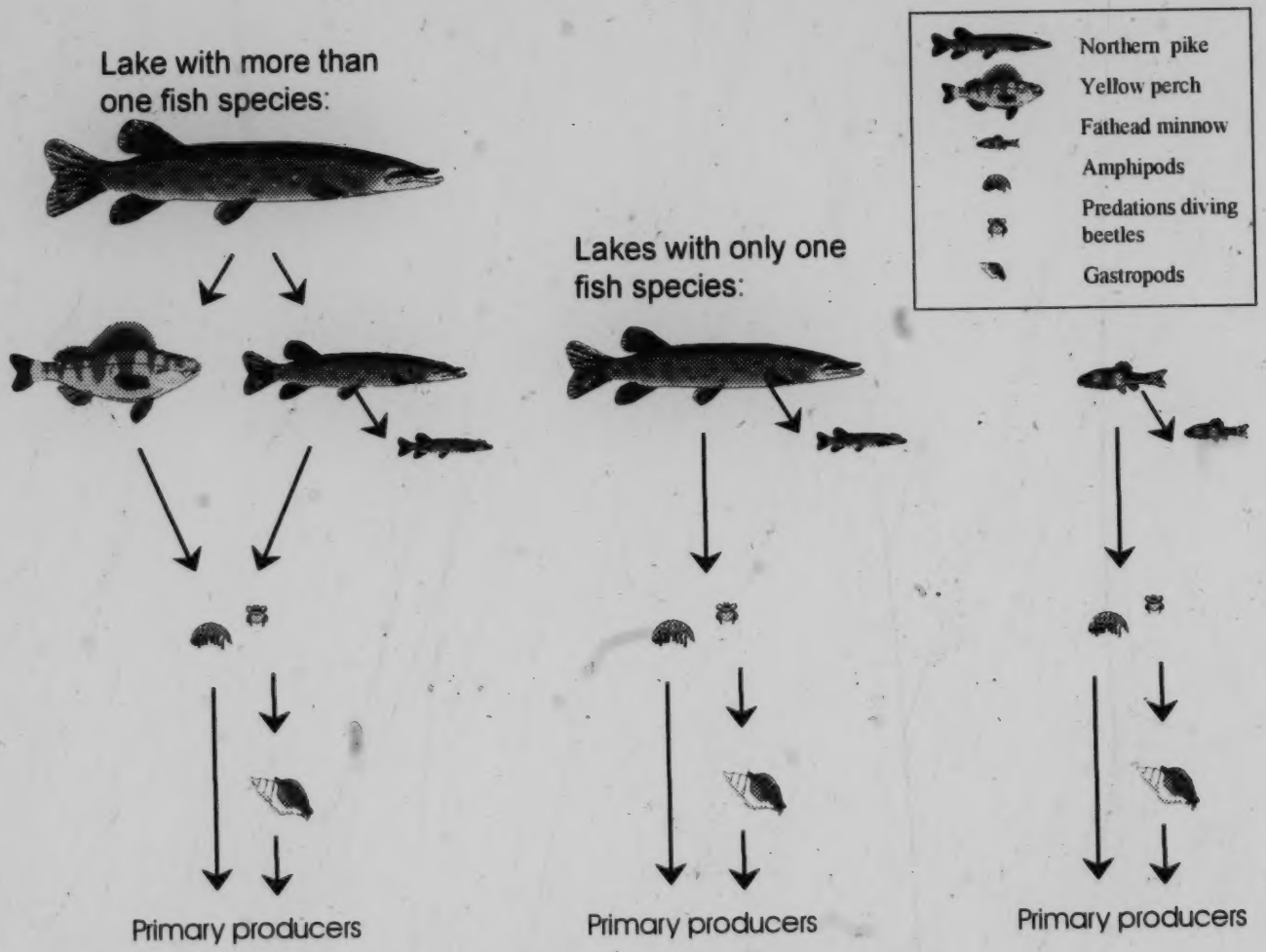

Figure 2-8: Conceptual model of food webs in lakes with different fish assemblages.

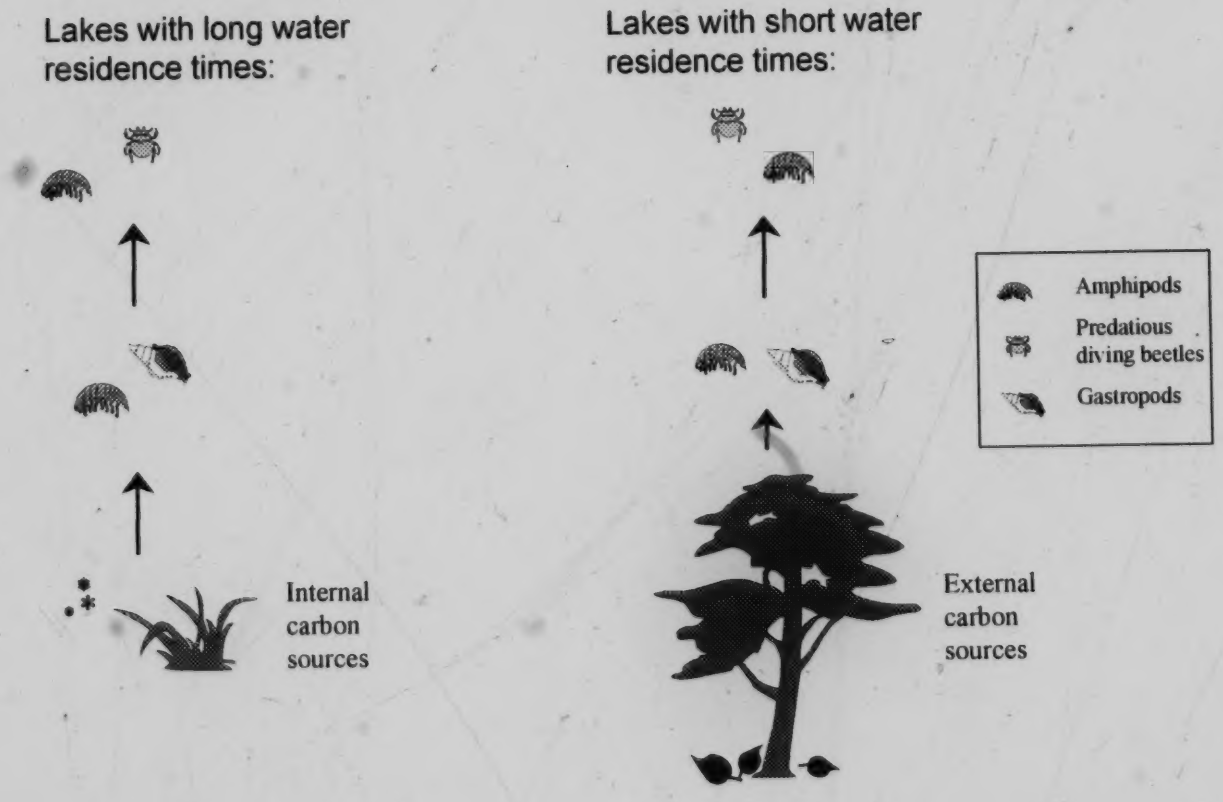

Figure 2-9: Conceptual model of carbon sources at the base of the food webs in lakes with long (>1yr) and short (≤1yr) water residence times.

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Chapter 3. DIET DIFFERENCES OF NORTHERN PIKE IN LAKES WITH DIFFERENT FISH ASSEMBLAGES: A STABLE ISOTOPE STUDY

Introduction

The general food habits of northern pike (*Esox lucius*) have been described several times (e.g., Frost 1954, Lawler 1965, Diana 1979, Bregazzi and Kennedy 1980, Chapman et al. 1989, Stephenson and Momot 1991, Sammons et al. 1994). It is commonly accepted that newly hatched northern pike feed almost exclusively on macroinvertebrates. After attaining lengths of 20-35 mm, fish constitute more of their diet as they grow until, at lengths >50 mm, fish usually become the sole prey of pike (Hunt and Carbine 1951, Frost 1954, Lawler 1965). Although Lawler (1965) documented northern pike (35-85 mm) that fed on zooplankton, diets of pike >85 mm were again mainly of fish. Therefore, large northern pike are usually considered to be piscivores.

However, there are studies showing that adult pike are not always exclusively piscivorous. Stephenson and Momot (1991) stated that although adult pike are mainly piscivores, they will continue to eat invertebrates opportunistically. Going further, Chapman et al. (1989) suggested that pike remain flexible with respect to their diet throughout their lives, with their feeding strategies changing in response to the availability of prey items.

In north-central Alberta, there are relatively few fish species in small lakes compared with many areas in north-central North America (e.g., Wisconsin, Tonn and Magnuson 1982; Ontario, Jackson and Harvey 1989). The low numbers of fish species can be explained not only by the small sizes of these lakes, but also by the increase in climatic severity at higher latitudes, and by the lakes' great distance from major glacial refugia, such as the Mississippi River (Nelson and Paetz 1992). Despite low species richness, small lakes in northern Alberta are dominated by two distinct fish assemblage types, one characterized by small-bodied omnivores such as fathead minnows (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*), and a second characterized by larger-bodied carnivores, including northern pike and yellow perch

(*Perca flavescens*) (Robinson and Tonn 1989). Due to the piscivorous nature of northern pike, small-bodied fishes are generally absent in the presence of pike.

In these boreal lakes, northern pike can sometimes be the only fish species present, perhaps because among the large-bodied species found in these lakes, the tolerance of pike to severe environments (i.e., hypoxic waters) is relatively high (Magnuson and Karlen 1970). There are very few studies on the feeding habits of pike in lakes with no other fish species present. Due to the absence of prey fish, I expected that macroinvertebrates would be a large component of pike diets in "pike-only" lakes compared with lakes where prey fish are present ("pike-other" lakes). Cannibalism is also a possibility because it tends to occur when food quality and/or quantity is low (Smith and Reay 1991). I used stable isotope analysis (SIA) and stomach content analysis (SCA) to compare the feeding habits of northern pike in "pike-only" lakes with those in lakes that also contain yellow perch and white sucker. SIA provides information about a fish's long-term assimilated diet (Gearing 1991), whereas SCA complements SIA by showing directly what a fish has consumed, but only shortly before capture. A second objective was to test if, and how, food habits of pike changed, as they grew in "pike-only" lakes and lakes that contained pike and other fish species. The use of SIA and SCA in this study should provide information on the flexibility of the feeding ecology of northern pike in lakes of the Boreal Plain Ecoregion.

Materials and Methods

Description of study lakes

The lakes in this study are located in the mixed-wood boreal forest of north-central Alberta (Fig. 3-1). Five study lakes were chosen based on the fish communities present. Two lakes, C17 and R4, contained only northern pike. During several initial samplings, SPH200 also contained only northern pike, but when an upstream beaver dam was breached in spring 1996, a very small population of brook stickleback was introduced briefly into the lake (they disappeared later in the summer). Still, I consider SPH200 a "pike-only" lake for the purposes of this study because brook stickleback were collected at no other time during the study. In two lakes, pike co-occurred with larger-

bodied prey fish. LLB20 contained northern pike and yellow perch, whereas SPH20 contained northern pike, yellow perch, and white sucker (*Catostomus commersoni)*. The study lakes are all small, shallow, and their trophic status range from mesotrophic to eutrophic (based on total phosphorus, Wetzel 1983) (Table 3-1).

Methods

At SPH200 (one of the "pike-only" lakes), northern pike were collected at three different times (May, June and August) during summer 1996, whereas in the other four study lakes, pike were collected only once in August or September of that year. Five to 10 gillnets were set overnight in each lake for 8 to 10 hour sets. The multi-mesh gillnets used were 1.5 x 42.7 m, with the following barmesh sizes: 6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, and 75 mm. Total length (TL) was recorded and muscle tissue was removed from each fish for stable carbon and nitrogen isotope analysis (SIA). Prior to SIA of fish samples, lipids in the muscle tissue were removed because lipids in fish muscle tissue may be depleted in ^{13}C and affect ecological interpretations (Kling et al. 1992). To remove lipids, samples were placed in a 1:1 methanol:chloroform solution for three 10 minute intervals and then freeze-dried. To homogenize the samples, freeze-dried tissues were ground with a mortar and pestle. Potential prey items of pike were also collected for SIA in SPH200, LLB20, and SPH20 (Chapter 2).

All samples were analyzed for stable carbon and nitrogen ratios on a Micromass Optima continuous flow mass spectrometer (CF-IRMS) directly coupled to a Carlo Erba NA1500 elemental analyzer and Autosampler at the National Hydrology Research Institute (Saskatoon, SK) (Chapter 2). Stable isotope data are presented as the relative difference between ratios of the sample and standard gases. The relative difference in stable carbon or nitrogen ratios between samples and standards is expressed by a differential notation called delta (δ): $\delta R(‰) = [(R_{sample}/R_{standard})/R_{standard}] \times 10^3$ where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $\delta^{13}C$ or $\delta^{15}N$ is the permil (‰) deviation of that sample from the recognized isotope standard, PeeDee Belemnite (PDB) limestone for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$ (Gearing 1991).

For subsequent statistical analyses, fish were separated into two size-classes: large (>85 mm TL) and small ≤85 mm TL) (based conservatively on the length at which pike have been documented to eat only fish; Frost 1954, Hunt and Carbine 1951, Lawler 1965). In SPH200, where large and small pike were captured, differences in isotopic signatures among pike size-classes were examined using t^*-tests for samples with heterogeneous variances. For all lakes, linear regressions were calculated to determine any relationship between isotope signatures and total length. All statistical analyses were conducted on SPSS (Norusis 1997).

For stomach content analyses (SCA), the digestive tract of each fish was removed, and frozen shortly after collection. Fish stomach contents were sorted taxonomically, counted, and weighed. In one case, a very large (~ 1m) pike that had recently ingested another pike was captured. This prey fish's total length was measured and its mass was calculated using a length-mass regression. For pike in the large size-class, frequency of occurrence and the percentage composition of prey taxa by number (percent number) and percentage composition of prey taxa by mass (percent mass) were calculated. For small northern pike, only frequency of occurrence and percent number were calculated. Frequency of occurrence is the percentage of all fish stomachs in which a particular prey taxon was found (Bowen 1996). Percent number is the percentage a particular prey taxon is contributing to the total number of food items in all stomachs (Bowen 1996). Percent mass is the percentage a particular prey taxon is contributing to the total mass of food in all stomachs (Bowen 1996). The number of fish stomachs containing food was often quite small; only stomachs containing prey items were used in the analysis. Digested remains of fish prey, such as scales, pharyngeal arches or other bones, were used to identify ingested prey items when possible. However, these prey items and unidentifiable organic matter or macrophytes that could not be quantified were not included the above calculations.

Results

Stable isotope signatures of potential prey items of pike were available only from three of the lakes, SPH200 ("pike-only" lake), LLB20 ("pike-perch" lake), and SPH20

("pike-other" lake). Since stable isotope signatures of potential prey items were not available for R4 and C17, it was not possible to assess diets of pike based on SIA. However, the isotopic signatures of pike in C17 and R4 were comparable to those of pike in SPH200 (Table 3-2). In SPH200, diets of large northern pike consisted of smaller pike and various littoral invertebrates (Chapter 2). Small pike also appeared to feed on invertebrates from the littoral zone. Based on SIA, large pike occupied a higher trophic level than small pike. In LLB20, based on SIA, diets of large northern pike consisted of invertebrates and fish (perhaps pike) as well (Chapter 2). In SPH20, isotopic signatures of pike suggested a diet of white sucker, and possibly small pike and invertebrates (Chapter 2). Based on SIA, diets of pike in SPH200, LLB20, and SPH20 consisted of invertebrates and fish.

SCA generally complemented SIA. In SPH200, SCA indicated that almost all large pike stomachs analyzed contained invertebrates, but relatively few contained fish (Table 3-3). Odonates and amphipods were the most common invertebrates consumed, and smaller pike were the most common fish prey for large northern pike (Table 3-4), although a few brook stickleback were found in their stomachs in early August. Numerically many more invertebrates were consumed by pike in SPH200 than fish, however, the percent mass of fish in the large pike stomachs was greater than that of invertebrates (Table 3-3). In R4 and C17, invertebrates (mostly odonates or amphipods) were the only prey items consumed by the large pike sampled (Table 3-4). In LLB20, the frequencies of occurrence of both invertebrates and fish were similar in large pike, however, invertebrates were consumed in considerably higher numbers than fish (Table 3-3). Most of the invertebrates consumed were amphipods, and the most common fish preyed upon was northern pike (Table 3-4). As in SPH200, although pike in LLB20 consumed invertebrates in high numbers, most of the prey mass was fish (Table 3-4). In SPH20, again large pike consumed more invertebrates than fish, but most of the prey mass was fish (Table 3-3). The most common invertebrate prey items of pike in SPH20 were odonates, and yellow perch were their most common prey fish (Table 3-4). Thus, although invertebrates were a numerically significant component of the large pike's diets

in all lakes, fish contributed most significantly to the prey mass in SPH200, LLB20, and SPH20.

Although I attempted to collect small pike (≤ 85 mm) in all lakes, I only caught a few in SPH200. These small pike had lower $\delta^{15}N$ signatures than large pike ($P<0.0001$) (Table 3-5), which suggested that small pike occupied a lower trophic level than large pike. However, there was no detectable difference between their carbon isotope signatures ($P=0.7$) (Table 3-5), which suggested that large and small pike had similar carbon sources. Based on SCA, 100% of the prey small pike consumed were invertebrates, with amphipods being most numerous. Chaoborids, few of which were found in stomachs of large pike, were also abundant in the stomachs of small pike. Although small pike consumed only invertebrates and were at a lower trophic level than large pike in SPH200, the carbon source of small and large pike appeared to be the same.

Although direct comparisons between small and large pike could not be done in all study lakes, there were indications that $\delta^{15}N$ and/or $\delta^{13}C$ of pike increased with increasing total length of pike, depending on the fish community present. There was a positive linear relationship between $\delta^{15}N$ and total length of northern pike in two of the "pike-only" lakes, SPH200 ($P<0.0001$) and R4 ($P<0.0001$) and nearly so in C17 ($P=0.05$) (Table 3-5). Interestingly, there was no linear relationship between $\delta^{15}N$ and total length of pike in the lakes that contained established populations of perch, LLB20 ($P=0.6$) and SPH20 ($P=0.1$) (Table 3-5). There was no linear relationship between $\delta^{13}C$ signatures and total length of northern pike in SPH20 ($P=1.0$), nor were there in LLB20 ($P=0.8$) and SPH200 ($P=0.2$) (Table 3-5). However, there was a positive linear relationship between $\delta^{13}C$ and total length in two of the "pike-only" lakes, R4 ($P<0.0001$) and C17 ($P<0.0001$) (Table 3-5), which suggested a change in diet as pike grew longer. Therefore, $\delta^{15}N$ tended to increase as pike grew larger in the "pike-only" lakes, and $\delta^{13}C$ increased as pike grew larger in R4 and C17, two of the "pike-only" lakes.

Discussion

SCA generally supported SIA in each study lake except SPH20 ("pike-other" lake). SIA and SCA supply different, but complementary, information on the diets of fish. Isotopic signatures reflect diets of pike integrated over the past year (Hesslein et al. 1993), whereas SCA indicates what an organism consumed just prior to being captured (Gearing 1991). In contrast to the SIA results in SPH20, few, if any, white suckers were found in the pikes' stomachs. The discrepancy between SIA and SCA may be explained by the small sample size of pike stomachs analyzed. For example, if few stomachs are analyzed, large, but infrequently eaten, white suckers could be missed in SCA of pike in SPH20, yet still be important to the annual diet, as reflected in the SIA. In the summer of 1996, when pike were captured, they likely consumed invertebrates simply because invertebrates were abundant. However, although invertebrates were consumed more frequently and in higher numbers than fish, fish contributed more to the nutrition of pike, as indicated by percent mass.

In contrast to pike in lakes that contained populations of prey fish, pike in the "pike-only" lakes had limited food choices: consume invertebrates or cannibalize smaller pike. Based on SIA and SCA, cannibalism by pike was evident in SPH200, one of the "pike-only" lakes. However, based on SCA, cannibalism was not evident in the two other "pike-only" lakes, R4 and C17. Instead, these two "pike-only" populations were apparently maintained on diets of invertebrates.

Cannibalism in pike has been reported in many studies (Hunt and Carbine 1951, Franklin and Smith 1963, Giles et al. 1986) and is thought to mainly occur when other food is scarce or unavailable, due to reduced access to prey refuges or insufficient prey numbers (Frost 1954, Smith and Reay 1991). Perhaps cannibalism was not evident in R4 and C17 because the pike caught in these lakes were smaller than their counterparts in other lakes, and the potential prey (small pike) were unavailable due to extensive macrophytes that were used by small pike as refuges. Alternatively, perhaps no fish were found in the pike stomachs simply due to the small number of stomachs analyzed; use of SIA for complementary information on long-term feeding habits was precluded by a lack of invertebrate (and small pike) samples.

When prey fish were present in lakes along with pike, it was expected that, compared with "pike-only" lakes, pike would consume other fish species more than other pike. Surprisingly, cannibalism was prevalent in LLB20 ("pike-perch" lake) with pike feeding on other pike more than perch. However, cannibalism appeared to be a fairly recent phenomenon in this lake because, as opposed to SPH200 ("pike-only" lake) and SPH20 ("pike-other" lake), SIA suggested that long-term feeding habits of pike were focused more on invertebrates than fish, even though recent diets included pike. Nevertheless, based on SCA, cannibalism was prevalent in the "pike-perch" lake.

The prevalence of cannibalism in LLB20 ("pike-perch" lake) may be explained by the size distribution and numbers of prey fish in the lakes. The catches per unit effort (CPUE) of pike in LLB20 and SPH20 ("pike-other" lake) were similar (0.4 and 0.5 fish/net/hour, respectively) but the CPUE of perch was much lower in LLB20 (0.4 fish/net/hour) than in SPH20 (3.0 fish/net/hour) (TROLS gill net surveys 1996). CPUE can be used in intra-specific comparisons as an indication of population density (Hubert 1996). Therefore, it appears that there were considerably fewer perch for the pike to catch in LLB20 compared to SPH20, which likely contributed to why pike in LLB20 consumed pike instead of perch. Also, perch were smaller (52-142 mm TL) in SPH20 than in LLB20 (57-327 mm TL) (TROLS gill net surveys, 1996). Therefore, it appears that pike feeding habits reflected prey availability. These results support Chapman et al. (1989), also working in lakes of the Boreal Plain Ecoregion, who suggested that northern pike are flexible in their feeding habits, and that the feeding flexibility of pike in northern lakes may be a result of the prey base and the seasonally dynamic nature of these lakes.

SIA was also used to detect indications of ontogenetic shifts in the diets of pike in these five boreal lakes. There was a positive linear relationship between $\delta^{15}N$ signatures and total length of pike in SPH200 and R4, and nearly so in C17 (all "pike-only" lakes), but there was no detectable relationship in LLB20 ("pike-perch" lake), or SPH20 ("pike-other" lake). This suggested that pike generally increased in trophic level as they grew in the "pike-only" lakes, but did not (over the range of sizes examined) in the lakes that contained pike and other prey fish. Hesslein and Ramlal (1993) found a general trend of increasing $\delta^{15}N$ signatures with increasing size of northern pike in the Athabasca River,

which has several fish species, and from this also suggested that larger pike occupied a higher trophic level than smaller pike. When Kiriluk et al. (1995) found no such relationship for lake trout (*Salvelinus namaycush*) in Lake Ontario, they suggested that the lake trout's opportunistic diet may have accounted for both the large range of $\delta^{15}N$ signatures among individual fish and the similar values among different age-classes. Opportunism in pike may account for the lack of relationship between $\delta^{15}N$ and length in LLB20 and SPH20 as well, especially in LLB20, where the large range in $\delta^{15}N$ signatures spanned two trophic levels regardless of fish length. In SPH20, smaller pike had similar $\delta^{15}N$ signatures as those of large pike. Thus, smaller pike appeared to occupy the same trophic level as larger pike in LLB20 or SPH20, in comparison with small pike in "pike-only" lakes which occupied lower trophic levels.

There were no positive linear relationships between $\delta^{13}C$ and total length of pike in SPH200 ("pike-only" lake), LLB20 ("pike-perch" lake) and SPH20 ("pike-other" lake). In LLB20, pike seemed to consume a variety of carbon sources. In SPH200 and SPH20, the carbon sources appeared to be the same for pike of all sizes. The lack of a linear relationship between total length and $\delta^{13}C$ in SPH200 (the only "pike-only" lake where no such relationship existed) indicates that although large and small pike were at different trophic levels in SPH200, they may consume organisms that use the same carbon source. Use of the same carbon source by small and large pike in SPH200 is supported by SCA because amphipods, or organisms that probably eat amphipods, were the primary food source for both size-classes of pike.

In contrast, there were positive linear relationships between $\delta^{13}C$ signatures and length in R4 and C17 ("pike-only" lakes). Kiriluk et al. (1995) found a correlation between $\delta^{13}C$ and age of lake trout, which reflected a switch in feeding from benthic to pelagic prey as the fish matured. A switch from pelagic to littoral feeding habits of pike may also explain the more negative $\delta^{13}C$ signatures of smaller pike relative to larger fish in C17 and R4. Based on SCA, only pike under 140 mm in R4 and C17 consumed Chaoboridae, which typically have relatively depleted $\delta^{13}C$ signatures, due to a pelagic food base (France 1995). There was evidence that pike altered their feeding habits from pelagic to littoral invertebrates as they grew longer.

In summary, invertebrates were a large component of pikes' diets in all lakes, especially in "pike-only" lakes. However, fish were important, to varying degrees in diets of pike in "pike-only" lakes, but particularly in lakes with other fish species present. Cannibalism was not necessarily more important in "pike-only" lakes, but appeared to be influenced by the relative availability of alternative prey, including invertebrates. There was evidence that trophic level of pike increased as length of pike increased in "pike-only" lakes. In contrast, smaller pike in lakes containing other fish species appeared to occupy the same trophic level as large pike. In R4 and C17, where, according to SCA, invertebrates were the sole food consumed by pike, there appeared to be a gradual transition from pelagic to littoral prey as pike grew, although in SPH200, their carbon source remained the same as they grew. In conclusion, this study indicates there is flexibility in the feeding habits of northern pike as their prey base changes.

Table 3-1: Physical, chemical, and biological parameters of the five study lakes, C17, R4, SPH200, LLB20 and SPH20, during summer 1996 (fish species: northern pike (np), yellow perch (yp), white sucker (ws), and brook stickleback (bs)).

Lake	Fish assemblage	Fish species	Location (N,W)	Bottom depth z_{max} (z_{mean}) (m)	mean summer pH	mean summer** total phosphorus (µg/L)
C17	"pike-only"	np	55°39', 111°55'	7.6 (1.8)	6.8	19+/-1
R4	"pike-only"	np	55°43', 110°43'	5.5 (1.0)	7.0	29+/-6
SPH200	"pike-only"	np, bs*	55°23', 113°38'	9.5 (4.1)	7.8	40+/-5
LLB20	"pike-perch"	np, yp	55°8', 111°45'	5.8 (2.1)	7.5	47+/-5
SPH20	"pike-other"	np, yp, ws	55°25', 113°42'	8.5 (4.4)	7.5	22+/-1

* only a few individuals of brook sticklebacks were caught in the June 1996 sampling

** mean summer total phosphorus was calculated for C17 and R4 with July, August and September values; whereas mean summer total phosphorus was calculated for SPH200, LLB20, and SPH20 with June, July and August values

Table 3-2: Means(+/-SE) and ranges of $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of northern pike in the study lakes, C17, R4, SPH200, LLB20 and SPH20, during summer 1996.

Fish assemblage	n	Size-class	δ^{13} C		δ^{15} N	
Lake			Mean+/-SE	Range	Mean+/-SE	Range
pike-only lakes						
C17	19	>85mm	-27.3+/-0.2	-28.6 to -25.0	12.8+/-0.1	11.0 to 13.9
R4	10	>85mm	-31.9+/-0.4	-34.4 to -30.2	10.2+/-0.2	9.0 to 10.8
SPH200	28	>85mm	-26.9+/-0.3	-28.9 to -26.7	11.4+/-0.3	8.9 to 13.8
	5	<85mm	-27.1+/-0.4	-28.5 to -26.2	9.2+/-0.2	8.7 to 9.6
pike-perch lake						
LLB20	18	>85mm	-27.0+/-0.5	-31.4 to -24.0	12.4+/-0.4	8.5 to 14.8
pike-other lake						
SPH20	14	>85mm	-25.4+/-0.3	-26.4 to -22.0	17.1+/-0.1	16.0 to 17.8

Table 3-3: Frequency of occurrence (% FO) and percentage by number and by mass of fish and invertebrates in the diets of northern pike in the five study lakes, C17, R4, SPH200, LLB20 and SPH20, during summer 1996.

Lake	Sample size	Size	Prey item	% FO	% Number	% Mass
C17	9	>85 mm	Invertebrates	100	100	100
R4	10	>85 mm	Invertebrates	100	100	100
SPH200	7	≤85 mm	Invertebrates	100	100	100
	38	>85 mm	Invertebrates	94.7	98.4	15.4
			Fish	21.1	1.5	84.5
LLB20	13	>85 mm	Invertebrates	50	97.8	24.4
			Fish	50	2.2	75.5
SPH20	13	>85 mm	Invertebrates	61.5	83.9	28.2
			Fish	23.1	16.1	71.7

Table 3-4: Frequency of occurrence (% FO) and percentage by number and by mass of prey taxa in the diet of northern pike in the five study lakes, C17, R4, SPH200, LLB20 and SPH20, during summer 1996.

Lake	Fish species	Item	% FO	% Number	% Mass
C17	Northern pike	**Invertebrates**			
	>85mm	Amphipoda	88.9	88.7	90.8
	n=9	Chaoboridae larvae	33.3	8.1	5.0
		Gastropoda	11.1	0.8	0.7
		Notonectidae	11.1	0.8	0.7
		Pelycepoda	11.1	0.8	0
		Zygoptera larvae	11.1	0.8	2.8
		Other			
		organic matter	44.4		
R4	Northern pike	**Invertebrates**			
	>85mm	Amphipoda	60.0	51.0	14.4
	n=10	Anisoptera larvae	90.0	26.9	83.3
		Chaoboridae larvae	10.0	15.9	0.1
		Coleoptera	10.0	2.1	0.3
		Gastropoda	20.0	1.4	0.3
		Hirudinea	10.0	0.7	0.3
		Nematomorpha	10.0	0.7	0.4
		Trichoptera larvae	10.0	0.7	1
		unidentified invertebrate	10.0	0.7	0
		Other			
		organic matter	10.0		
SPH200	Northern pike	**Invertebrates**			
	≤85mm	Amphipoda	75.0	50.0	na
	n=7	Chaoboridae larvae	25.0	42.3	na
		Chironomidae larvae	25.0	7.7	na
		Other			
		filamentous algae	12.5	1.9	
		organic matter	50.0		
SPH200	Northern pike	**Invertebrates**			
	>85mm	Amphipoda	71.1	80.3	4.2
	n=38	Anisoptera larvae	47.4	6.1	8.4
		Chaoboridae larvae	2.6	0.1	0
		Rotifera	2.6	0.1	0
		Trichoptera larvae	13.2	0.6	0.1
		unidentified invertebrate	7.9	0.4	1.1
		Zygoptera larvae	39.5	10.8	1.6
		Fish			
		Northern pike	10.5	0.6	84.2
		Brook stickleback	10.5	0.9	0.3
		Other			
		macrophytes	10.5		
		organic matter	5.3		

Table 3-4: (continued)

Lake	Fish species	Item	% FO	% Number	% Mass
LLB20	Northern pike	**Invertebrates**			
	>85mm	Amphipoda	38.5	95.9	22.2
	n=12	Anisoptera larvae	15.4	0.7	2.2
		Chironomidae larvae	7.7	0.7	0
		unidentified invertebrate	7.7	0.4	0
		Fish			
		Yellow perch	7.7	0.4	2.3
		Northern pike	23.1	1.1	71.1
		unidentified fish	15.4	0.7	2.1
		Other			
		scales	7.7		
		macrophytes	15.4		
		organic matter	15.4		
SPH20	Northern pike	**Invertebrates**			
	>85mm	Amphipoda	7.7	38.7	0.6
	n=13	Anisoptera larvae	30.8	12.9	22.8
		Chironomidae larvae	7.7	3.2	0.1
		Coleoptera	7.7	3.2	3.4
		Diptera	7.7	3.2	0
		Gastropoda	7.7	3.2	0
		Hirudinea	7.7	3.2	0.2
		Pelycepoda	7.7	12.9	0.3
		Trichoptera larvae	7.7	3.2	0.8
		Fish			
		Yellow perch	23.1	9.7	60.5
		Northern pike	7.7	3.2	4.5
		unidentified fish	7.7	3.2	6.7
		Other			
		spruce needles	15.4		
		Nostoc	7.7		
		organic matter	7.7		

Table 3-5: Linear relationships between $\delta^{15}N$ and $\delta^{13}C$ signatures (‰) and total length (mm) of northern pike in C17, R4, SPH200, LLB20 and SPH20.

Lake	Fish assemblage	Dependent variable	R^2	n	slope	*P*-value
C17	"pike-only"	$\delta^{15}N$	0.2	19	0.5	0.05
		$\delta^{13}C$	0.6	19	0.7	<0.0001
R4	"pike-only"	$\delta^{15}N$	0.8	10	0.9	<0.0001
		$\delta^{13}C$	0.9	10	0.9	<0.0001
SPH200	"pike-only"	$\delta^{15}N$	0.4	33	0.7	<0.0001
		$\delta^{13}C$	0.05	33	-0.2	0.2
LLB20	"pike-perch"	$\delta^{15}N$	0	18	-0.1	0.6
		$\delta^{13}C$	0.01	18	-0.1	0.8
SPH20	"pike-other	$\delta^{15}N$	0.2	14	0.7	0.1
		$\delta^{13}C$	0	14	0.001	1.0

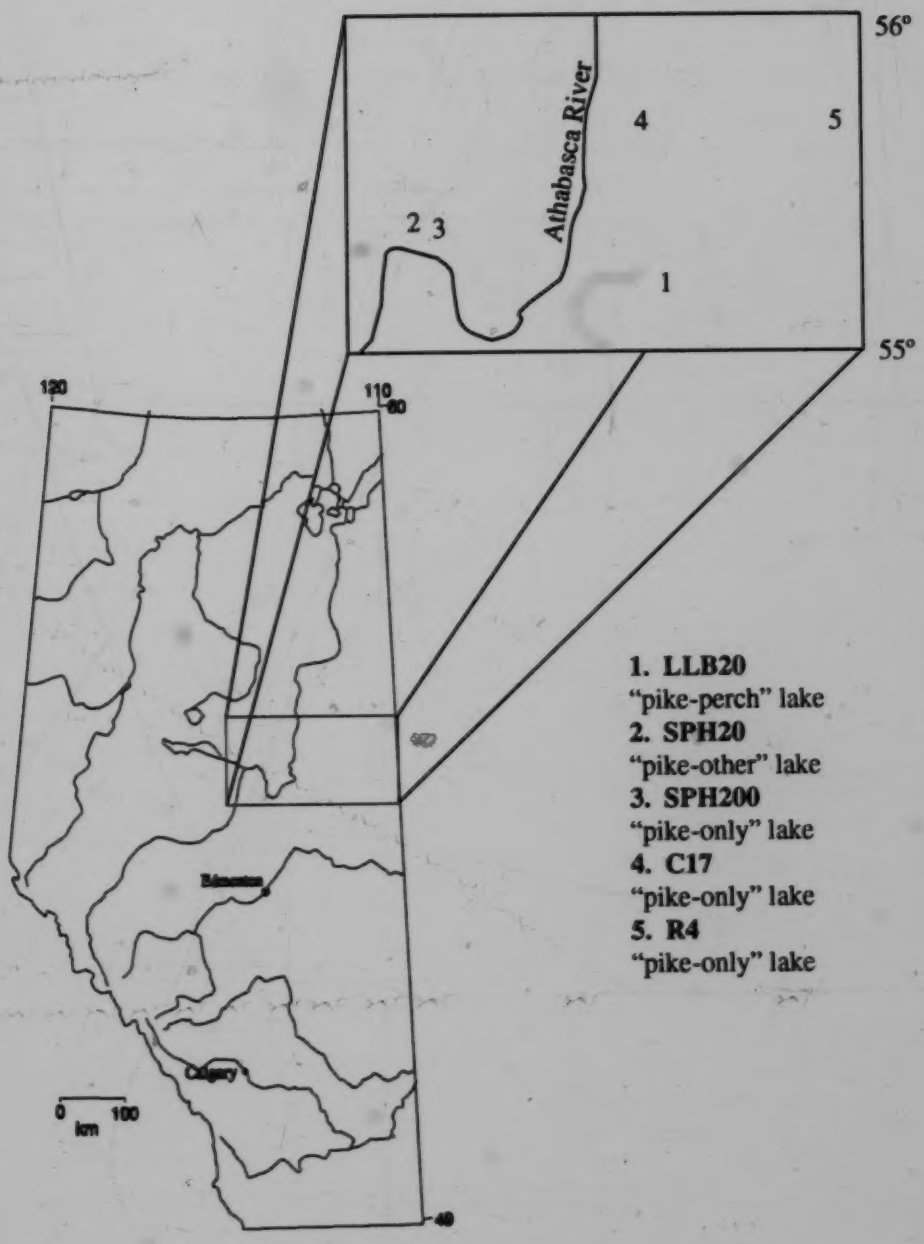

Figure 3-1: Alberta map showing the location of the study lakes.

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Chapter 4. GENERAL DISCUSSION AND CONCLUSIONS

In 1994, the Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) project began research in the boreal forest of Alberta to determine the effects of timber harvesting on terrestrial and aquatic ecosystems. Prior to the TROLS project, lakes of Alberta's boreal forest had not been studied for forestry impacts, nor had stable isotope analysis (SIA) been used to characterize food webs in these lakes. Lakes of Alberta's boreal forest are quite productive and shallow, and hence often support large amounts of macrophytes. Due to a high propensity for hypoxic conditions during winter and a low number of streams in the area, the lakes contain relatively few fish species. Also, for the most part, the lakes generally have relatively longer water residence times compared to those in other regions such as the boreal forest on the Precambrian Shield (Mitchell and Prepas 1990, Allan et al. 1994) due to relatively low amounts of precipitation in the region. Since lakes of the Alberta's boreal forest have been little studied, it was important to collect base-line data about the lakes prior to timber harvesting. My project was part of the pre-harvest phase of TROLS and was to serve as a base-line study.

Prior to my study, SIA had never been used to characterize food webs of these boreal lakes, but it has been effective in many other aquatic ecosystems around the world. Additionally, it has been suggested that SIA can be used as a simple biomonitoring tool to gauge the effects of land clearing on lotic food webs (Rounick et al. 1982, Winterbourn and Rounick 1985, Rounick and Winterbourn 1986, Doucett et al. 1996). The studies mentioned above were conducted on stream ecosystems where attached algae and terrestrial sources are the two most probable food sources for consumers. An increased role of algae in forest streams after logging has been shown to be detectable by SIA (Rounick et al. 1982, Winterbourn and Rounick 1985). The ability to detect the increased role of algae occurred only because the signatures of the algae were distinct from the terrestrial carbon source(s), and so the question of the utility of SIA in these lakes of the Boreal Plain Ecoregion arose.

A measurable isotopic distinction between external and internal carbon sources is necessary for SIA to be useful to determine trophic relationships and land clearing

impacts (Rounick et al. 1982). The less complicated the food web, the more likely SIA will be a useful tool to detect forestry impacts on carbon inputs and trophic changes. The food webs in these boreal lakes, however, are not simple (due to numerous potential carbon sources). External inputs in the study lakes include leaves from surrounding vegetation, and humus or litter from the forest floor, whereas internal inputs include phytoplankton, periphyton, bacteria and macrophytes. In my study lakes, large numbers of carbon sources, both internal and external, resulted in overlap in carbon isotope signatures of various taxa. Indistinct signatures of the carbon inputs translated into overlap of carbon isotope signatures of organisms at higher trophic levels. Therefore, SIA was not consistently useful at differentiating contributions of different carbon sources to consumers. More intensive study of the lower trophic levels of the food webs, including the part that heterotrophic microorganisms play in these shallow, eutrophic lakes, would be useful to elucidate which carbon sources are driving the food webs.

Overlap in $\delta^{13}C$ signatures is a common problem in isotopic studies (Rosenfeld and Roff 1992, France 1995). However, the use of multiple isotopes and/or other complementary data helps to resolve the difficulty of nondistinct isotopic signatures (Gearing 1991). In my study lakes, the use of $\delta^{15}N$, as well as $\delta^{13}C$, helped to differentiate between some carbon sources. SIA, along with SCA, was useful to determine trophic structure of the lake food webs, to compare feeding habits of pike in lakes with different fish assemblages, and to detect ontogenetic shifts in diet of pike. Discrepancies between SIA and SCA could be explained because SIA reflects an organism's diet over a longer time period (e.g., months), whereas SCA reflects only what an organism consumed just prior to being captured (Gearing 1991). Together, however, SIA and SCA provided information on the size and complexity of contrasting food webs.

For future studies of a similar nature, I would suggest that although only a few fish are needed to evaluate trophic relationships with SIA, a greater number of fish for SCA would be beneficial to detect ontogenetic shifts in the fish. I would also suggest that water residence times of lakes be considered in studies of similar nature. If the water residence times of the lakes are less than a year, a focus on potential carbon sources from

the surrounding watershed is important. However, if water residence times are greater than a year, then internal carbon sources will likely be more important.

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Appendix A:

Isotopic signatures of biota in SCL20 during summer 1996

Table A1: Isotopic signatures ((mean+/-SE)(n) or single values (‰)) of consumers in SCL20 during summer 1996.

	May		June	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
Fathead minnows	-28.1+/-0.2(5)	13.8+/-0.2(5)	-29.3+/-0.3(5)	14.5+/-0.4(5)
Littoral Invertebrates				
Odonata				
Anisoptera larvae	na	na	na	na
Zygoptera larvae	-29.5	7.7	na	na
Coleoptera				
Dytiscidae	-31.4	7.6	na	na
Coleoptera larvae	na	na	na	na
Hydrophilidae	-28.4	5.4	na	na
Hemiptera				
Corixidae	-25.5	4.6	-26.5	7.7
Hirudinea				
Erpobdellidae	-29.7	10.6	-27.3+/-1.5(2)	12.0+/-0.1(2)
Glossiphonidae	-24.2	11.2	-27.8	12.5
Trichoptera				
Limnephilidae larvae	-28.3+/-0.0(2)	6.8+/-1.0(2)	na	na
Molannidae larvae	-28.4	9.1	na	na
Phryganeidae larvae	-29.9	8.4	-27.4+/-0.5(2)	8.3+/-1.5(2)
Crustacea				
Amphipoda	-28.7+/-1.3(2)	6.9+/-0.3(2)	-26.7+/-0.8(2)	6.5+/-0.8(2)
Other				
Oligochaetae	-24.7	10.1	-32.3	9.8
Chironomidae larvae	-28.1	10.0	-30.3	10.9
Profundal/Pelagic Invertebrates				
Corixidae	na	na	na	na
Amphipoda	na	na	na	na
Copepoda	na	na	-35.7	6.1
Daphnidae	na	na	-29.5	10.2
Chaoboridae larvae	na	na	-27.5	13.4
Chaoboridae pupae	-29.6	9.5	na	na
Chironomidae larvae	na	na	na	na
Hydrachnidia	-30.8	12.5	-26.8	11.6
zooplankton x>500µm	na	na	na	na
zooplankton x>243µm	-30.5	9.9	-30.9+/-0.4(5)	9.6+/-0.3(5)
zooplankton <243µm	na	na	na	na

Table A1: (continued)

Organism	August		September	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
Fathead minnows	-25.9+/-0.2(30)	13.5+/-0.1(30)	-26.9+/-0.1(4)	13.7+/-0.3(4)
Littoral Invertebrates				
Odonata				
Anisoptera larvae	-25.6	10.0	na	na
Zygoptera larvae	na	na	na	na
Coleoptera				
Dytiscidae	na	na	na	na
Coleoptera larvae	-26.0	9.9	na	na
Hydrophilidae	na	na	-25.7	7.8
Hemiptera				
Corixidae	-25.3	7.9	-26.6	8.0
Hirudinea				
Erpobdellidae	-26.4+/-0.3(2)	10.4+/-0.7(2)	-26.7	10.8
Glossiphonidae	na	na	-26.1+/-0.8(2)	10.2+/-0.8(2)
Trichoptera				
Limnephilidae larvae	na	na	-25.4	6.8
Molannidae larvae	-28.2	11.2	-27.1	10.0
Phryganeidae larvae	-26.6+/-0.8(2)	8.0+/-0.7(2)	-21.8+/-0.4(2)	9.9+/-0.2(2)
Crustacea				
Amphipoda	-26.7+/-0.0(2)	6.7+/-0.9(2)	-26.3+/-0.5(2)	7.0+/-1.0(2)
Other				
Oligochaetae	na	na	na	na
Chironomidae larvae	na	na	-26.1	10.7
Profundal/Pelagic Invertebrates				
Corixidae	-27.1	9.4	-26.2	7.5
Amphipoda	na	na	-28.8	8.0
Copepoda	na	na	na	na
Daphnidae	na	na	na	na
Chaoboridae larvae	-26.5	11.8	na	na
Chaoboridae pupae	na	na	na	na
Chironomidae larvae	-23.9	9.8	na	na
Hydrachnidia	-28.0	12.3	na	na
zooplankton x>500μm	-29.3+/-0.2(3)	8.8+/-0.5(3)	na	na
zooplankton x>243μm	-30.0+/-0.5(2)	8.0+/-0.4(2)	-27.5+/-0.1(4)	10.8+/-0.2(4)
zooplankton <243μm	-26.6	10.5	-33.5+/-3.7(2)	9.5+/-1.5(2)

Table A2: Isotopic signatures ((mean+/-SE)(n) or single values (‰)) of primary in SCL20 during summer 1996.

	May		June	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
epiphytes	na	na	-16.7	4.2
phytoplankton x>63 µm	-32.0	8.8	na	na
POM	-32.1+/-0.3(2)	6.4+/-0.2(2)	-29.5	10.8
Porifera	na	na	na	na
bryophytes	-27.1	1.5	na	na
Alisma sp.	na	na	-25.0	0.1
Cladophora sp.	na	na	na	na
Equisetum sp.	na	na	na	na
Nuphar sp.	na	na	-24.7	2.3
Potamogeton sp.	na	na	-12.5	6.9
Polygonum sp.	na	na	na	na
Scirpus sp.	na	na	na	na
profundal detritus	-31.1+/-0.2(2)	2.2	-31.3+/-0.1(2)	4.6+/-0.2(2)
littoral detritus	-27.7	1.4	na	na
terrestrial matter	na	na	na	na

Table A2: (continued)

	August		September	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
epiphytes	-26.6	5.3	na	na
phytoplankton x>63 µm	na	na	na	na
POM	-20.5+/-0.2(4)	3.3+/-0.7(4)	-30.0+/-0.7(2)	3.1+/-0.9(2)
Porifera	-28.3	5.9	-20.3	5.5
bryophytes	na	na	-26.5	5.2
Alisma sp.	na	na	na	na
Cladophora sp.	-21.5	3.3	na	na
Equisetum sp.	na	na	na	na
Nuphar sp.	-24.9	4.6	-25.4	2.0
Potamogeton sp.	-15.9	8.2	na	na
Polygonum sp.	na	na	-28.3	3.7
Scirpus sp.	-27.4	5.3	na	na
profundal detritus	-30.6+/-0.2(2)	5.2 +/- 0.0 (2)	-31.4+/-0.0(2)	2.4+/-0.4(2)
littoral detritus	-27.9	4.2	-27.1	3.0
terrestrial matter	na	na	na	na

Appendix B:

Isotopic signatures of biota in SPH200 during summer 1996

Table B1: Isotopic signatures ((mean+/-SE)(n) or single values (‰)) of consumers in SPH200 during summer 1996.

	May		June	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
N. pike <85mm	na	na	-27.1+/-0.4(5)	9.2+/-0.2(5)
N. pike >85mm	-27.5	12.2	-27.2+/-0.3(6)	11.8+/-0.5(6)
Br. stickleback	na	na	-29.9+/-0.2(4)	11.5+/-0.1(4)
Littoral Invertebrates				
Odonata				
Anisoptera larvae	-29.2+/-0.3(2)	7.6+/-0.6(2)	-29.3+/-0.6(2)	6.4+/-0.5(2)
Zygoptera larvae	-26.8	5.6	-28.6	9.4
Ephemeroptera				
Caenidae	na	na	-26.5	5.1
Hemiptera				
Corixidae	-29.8	4.6	-26.6	6.5
Notonectidae	-28.2	6.4	-31.2	9.7
Coleoptera				
Dytiscidae	-29.1+/-0.4(2)	6.4+/-0.7(2)	-27.2+/-0.2(2)	7.6+/-0.3(2)
Dytisicdae larvae	na	na	-28.3	6.4
Hydrophilidae	na	na	na	na
Hirudinea				
Erpobdellidae	na	na	-26.7	7.7
Glossiphonidae	-30.0	9.4	-27.3	7.4
Trichoptera				
Glossosomatidae larvae	-29.1	7.8	na	na
Limnephilidae larvae	na	na	-26.4	6.5
Phryganeidae larvae	-31.0	6.3	-27.0	5.6
Rhyacophilidae larvae	na	na	na	na
Trichoptera larvae	na	na	na	na
Gastropoda				
Lymnaedae	na	na	na	na
Physidae	-29.3	5.6	-27.7	6.9
Planorbidae	-26.1	4.9	-27.0	5.3
Crustacea				
Amphipoda	na	na	-28.0	3.7
Others				
Chironomidae larvae	na	na	-27.7	4.8
Hydrachnidia	na	na	na	na
Profundal/Pelagic Invertebrates				
Daphnidae	na	na	-35.5+/-0.1(4)	9.8+/-0.1(4)
Copepoda	na	na	-32.8	12.2
Chironomidae larvae	-32.0	6.1	-32.5	5.1
Chaoboridae larvae	-34.6	9.2	-33.4+/-1.1(3)	9.3+/-0.1(3)
Chaoboridae pupae	na	na	-33.4	11.1
zooplankton x<500 µm	na	na	na	na
zooplankton x>500 µm	na	na	na	na
Hydrachnidia	-29.8	8.8	-29.3	8.3

Table B1: (continued)

Organism	August		September	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
N. pike <85mm	na	na	na	na
N. pike >85mm	-26.8+/-0.3(22)	11.2+/-0.3(22)	na	na
Br. stickleback	na	na	na	na
Littoral Invertebrates				
Odonata				
Anisoptera larvae	-23.7	7.1	-27.4	8.0
Zygoptera larvae	-26.0	8.5	-26.7	7.3
Ephemeroptera				
Caenidae	na	na	na	na
Hemiptera				
Corixidae	-28.7	7.7	-27.5	4.5
Notonectidae	-28.8+/-0.2(2)	8.6+/-0.3(2)	-30.2	7.5
Coleoptera				
Dytiscidae	-28.8	7.2	na	na
Dytisicdae larvae	na	na	na	na
Hydrophilidae	na	na	-26.9+/-0.8(2)	4.9+/-0.3(2)
Hirudinea				
Erpobdellidae	na	na	-27.4	7.7
Glossiphonidae	na	na	na	na
Trichoptera				
Glossosomatidae larvae	na	na	na	na
Limnephilidae larvae	-22.36	5.28	-26.7	5.0
Phryganeidae larvae	na	na	na	na
Rhyacophilidae larvae	na	na	-25.7	6.5
Trichoptera larvae	na	na	-26.0	6.8
Gastropoda				
Lymnaedae	-23.6	6.1	-25.6	5.5
Physidae	-25.0	5.4	-27.5	5.0
Planorbidae	-24.6+/-0.2(2)	7.2+/-2.1(2)	-25.7	4.6
Crustacea				
Amphipoda	-24.8+/-0.3(2)	5.2+/-0.3(2)	-26.2	4.8
Others				
Chironomidae larvae	-25.2	7.4	-24.2	5.4
Hydrachnidia	-28.4	14.4	na	na
Profundal/Pelagic Invertebrates				
Daphnidae	na	na	na	na
Copepoda	na	na	na	na
Chironomidae larvae	na	na	na	na
Chaoboridae larvae	na	na	na	na
Chaoboridae pupae	na	na	na	na
zooplankton x<500 μm	-33.4	9.2	na	na
zooplankton x>500 μm	-35.0	10.1	na	na
Hydrachnidia	-25.6	6.7	na	na

Table B2: Isotopic signatures ((mean+/-*SE*)(n) or single values (‰)) of primary producers in SPH200 during summer 1996.

	May		June	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
epiphytes	na	na	-27.6	1.8
Nostoc	na	na	-19.7	1.3
phytoplankton x<250 µm	na	na	na	na
phytoplankton x>64 µm	na	na	-32.2+/-0.1(4)	6.1+/-0.1(4)
POM	-35.0+/-0.7(3)	7.9+/-0.7(3)	na	na
Sagittaria sp.	na	na	na	na
Ceratophyllum sp.	-21.7	0.4	-18.3	2.6
Myriophyllum sp.	na	na	na	na
Potamogeton zosteriformis	-13.5	-4.2	-15.4	2.5
Potamogeton richardsonii	na	na	-14.4	-3.5
Nuphar sp.	-23.1	0.8	-23.4	-0.2
Chara sp.	na	na	-23.0	0.6
Cladophora sp.	na	na	-23.8	4.3
Rhizoclonium sp.	na	na	na	na
Lemna sp.	na	na	na	na
Polygonum sp.	na	na	na	na
Typha sp.	na	na	na	na
profundal detritus	-31.6+/-0.0(2)	0.9+/-0.4(2)	-32.0+/-0.1(2)	2.9+/-0.2(2)
littoral detritus	na	na	na	na
terrestrial matter	na	na	na	na

Table B2: (continued)

	August		September	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
epiphytes	na	na	na	na
Nostoc	na	na	na	na
phytoplankton x<250 µm	-31.6+/-0.3(3)	4.7+/-0.7(3)	na	na
phytoplankton x>64 µm	na	na	na	na
POM	na	na	na	na
Sagittaria	-25.1	3.0	-25.7	4.3
Ceratophyllum	na	na	-15.5	0.1
Myriophyllum	na	na	-15.5	3.0
Potamogeton zosteriformis	-11.7	-5.4	na	na
Potamogeton richardsonii	-12.6	-2.4	na	na
Nuphar	-23.8	-0.6	-25.2	2.9
Chara	na	na	na	na
Cladophora	na	na	na	na
Rhizoclonium	-17.8	0.7	na	na
Lemna	na	na	-20.6	4.4
Polygonum	na	na	-28.5	1.5
Typha	na	na	-28.1	3.3
profundal detritus	-31.4	2.7	na	na
littoral detritus	-27.3	2.1	-27.1+/-0.3(2)	1.3+/-0.2
terrestrial matter	na	na	-28.1+/-0.1(4)	-0.1+/-0.4(4)

Appendix C:

Isotopic signatures of biota in LLB20 and SPH20 during summer 1996

Table C1: Isotopic signatures ((mean+/-SE)(n) or single values (‰)) of consumers in LLB20 and SPH20 during summer 1996.

	LLB 20		SPH 20	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
N. pike >85mm	-27.0+/-0.4(18)	12.4+/-0.4(18)	-25.4+/-0.3(14)	17.1+/-0.1(14)
Y.perch <150mm	-28.7+/-0.4(6)	12.8+/-0.4(6)	-28.1 +/- 0.1(12)	16.7 +/- 0.2(12)
Y.perch >150mm	-27.2+/-0.2(11)	11.2+/-0.3(11)	na	na
W.sucker	na	na	-26.1+/-1.2(2)	14.7+/-1.1(2)
Littoral Invertebrates				
Odonata				
Anisoptera larvae	-28.5	9.1	-22.5	9.4
Zygoptera larvae	-29.4	10.1	-23.3	10.1
Coleoptera			na	na
Dytiscidae	-28.9	7.9	na	na
Hydrophilidae	-32.0	6.3	-27.6	7.9
Hemiptera				
Corixidae	-33.2	7.8	-25.7	10.6
Notonectidae	-29.5	10.0	-27.10+/-0.0(2)	10.2+/-0.3(2)
Hirudinea				
Erpobdellidae	-27.5	10.2	-25.5	12.8
Glossiphonidae	-29.2	10.3	na	na
Trichoptera				
Limnephilidae larvae	-26.7	7.9	-22.5	5.4
Phryganeidae larvae	na	na	-29.2	8.5
unidentified Trichoptera	na	na	-23.2	8.0
Gastropoda				
Lymnaeidae	na	na	-19.0	4.0
Physidae	-31.2	7.4	-24.9	2.5
Planorbidae	-29.7	8.5	-24.3	9.6
Crustacea				
Amphipoda	-28.9+/-0.4(2)	6.6+/-0.5(2)	-25.8+/-0.3(2)	7.2+/-0.4(2)
Daphnidae	-37.3+/-0.5(4)	5.3+/-0.7(4)	-29.7+/-0.1(3)	10.0+/-0.6(3)
Other				
Oligochaetae	na	na	-24.5	7.7
Chironomidae larvae	-30.3	6.3	-24.0	6.1
Hydrachnidia	-25.4	8.6	na	na
Profundal/Pelagic Invertebrates				
Chaoboridae larvae	-30.7+/-0.5(2)	10.5+/-0.6(2)	-30.2+/-0.2(4)	9.8+/-0.1(4)
Chironomidae larvae	-32.4	7.6	-29.0	8.9
Hydrachnidia	-32.7	8.7	na	na
zooplankton x>243µm	-35.8+/-2.0(2)	8.1+/-1.8(2)	na	na

Table C2: Isotopic signatures ((mean+/-SE)(n) or single values (‰)) of primary producers in LLB20 and SPH20 during summer 1996.

	LLB 20		SPH 20	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
phytoplankton x>64 µm	-23.2+/-0.2(2)	4.6+/-0.3(2)	-27.5+/-1.9(2)	7.1+/-0.8(2)
POM	-27.0+/-0.5(2)	3.4+/-0.1(2)	na	na
epiphytes	na	na	-15.9	1.3
Planctonema sp.	na	na	-17.7	6.0
Chaetophora sp.	na	na	-18.8	2.7
Rhizoclonium sp.	na	na	-20.3	2.3
Cleotrichia sp.	na	na	-19.0	-0.5
Equisetum sp.	na	na	-25.4	8.8
Scirpus sp.	na	na	-27.8	6.9
Typha sp.	na	na	-26.7	8.3
Lemna trisulca	-20.6	0.9	-26.7	6.2
Nuphar sp.	-23.1	2.2	-24.2	9.4
Polygonum sp.	-27.2	4.0	-26.3	7.1
Sagittaria sp.	na	na	-26.9	4.0
Ceratophyllum sp.	-18.7	4.4	-13.01	6.9
Myriophyllum sp.	-20.1	2.4	na	na
Potamogeton zosteriformis	-19.6	1.3	na	na
Potamogeton richardsonii	na	na	-16.9	4.4
Potamogeton vaginatus	na	na	-10.8	6.9
bryophytes	na	na	-35.4	0.8
littoral detritus	-27.8	3.5	-25.9	2.4
profundal detritus	-29.0+/-0.2(2)	3.7+/-0.6(2)	-29.6+/-0.1(2)	4.4+/-0.5(2)
terrestrial matter	-28.9+/-0.5(6)	2.7+/-0.9(6)	-28.6+/-0.6(4)	0.3+/-0.4(4)

Appendix D:

Isotopic signatures of biota in LLB800 during summer 1996

Table D1: Isotopic signatures ((mean+/-SE)(n) or single values (‰)) of consumers in LLB800 during summer 1996.

	May		June	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
Yellow perch	na	na	-22.2	13.9
Amphibians				
Bufo tadpole	na	na	-22.8	9.5
Rana tadpole	na	na	-23.4	8.9
Littoral Invertebrates				
Odonata				
Anisoptera larvae	na	na	-27.2	7.4
Zygoptera larvae	-20.9	10.5	-22.2	12.8
Coleoptera				
Chrysomelidae	na	na	-26.6	8.7
Gyrinidae	-24.4	7.3	-23.0	8.8
Hydrophilidae	na	na	na	na
Dytiscidae	-24.1	9.6	-21.9	9.3
Coleoptera larvae	na	na	-21.3	10.2
Hemiptera				
Corixidae	-25.6	5.3	-24.8	8.7
Notonectidae	-23.1	6.4	-23.3	7.7
Hirudinea				
Erpobdellidae	-23.2	11.1	-21.6	12.2
Glossiphonidae	-20.6	10.4	-19.1	10.7
Trichoptera				
Limnephilidae larvae	na	na	-21.4+/-0.1(2)	10.6+/-1.1(2)
Molannidae larvae	na	na	na	na
Phryganeidae larvae	na	na	-22.6	11.4
Gastropoda				
Lymnaeidae	na	na	-14.5	7.8
Physidae	-21.5	9.3	-19.5	9.2
Planorbidae	-19.0	6.7	-16.9	6.4
Crustacea				
Amphipoda	-25.9	10.8	-24.2	9.9
Other				
Chironomidae larvae	-24.7	7.9	na	na
Profundal/Pelagic Invertebrates				
Corixidae	na	na	na	na
Amphipoda	na	na	na	na
Chaoboridae larvae	-22.5	12.0	na	na
Chaoboridae pupae	-23.9	9.7	na	na
Chironomidae larvae	-25.7	9.0	-28.7	10.8
Daphnidae	na	na	-23.3+/-0.1(6)	8.8+/-0.2(6)
Hydrachnidia	-22.8	10.0	-24.8	12.2
zooplankton x>243 µm	na	na	-22.6	8.4

Table D1: (continued)

	August		September	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
Yellow perch	na	na	na	na
Amphibians				
Bufo tadpole	na	na	na	na
Rana tadpole	na	na	na	na
Littoral Invertebrates				
Odonata				
Anisoptera larvae	na	na	na	na
Zygoptera larvae	-21.0	11.6	-21.9	10.5
Coleoptera				
Chrysomelidae	na	na	na	na
Gyrinidae	na	na	na	na
Hydrophilidae	na	na	-24.7	5.0
Dytiscidae	-23.6	10.3	-22.3	8.4
Coleoptera larvae	-25.0+/-0.3(2)	9.8+/-0.9(2)	na	na
Hemiptera				
Corixidae	-22.8	8.1	-24.6	6.8
Notonectidae	-24.0+/-0.1(2)	9.8+/-0.8(2)	-25.2	7.9
Hirudinea				
Erpobdellidae	-22.7	12.7	-22.5	11.7
Glossiphonidae	-22.0+/-0.9(2)	12.0+/-0.5(2)	-15.6	11.9
Trichoptera				
Limnephilidae larvae	na	na	na	na
Molannidae larvae	-18.9	10.5	na	na
Phryganeidae larvae	na	na	-21.5	13.1
Gastropoda				
Lymnaeidae	-18	7.0	-17.7	8.0
Physidae	-16.7	7.6	-22.6	7.4
Planorbidae	-19.6	7.5	-18.0	6.3
Crustacea				
Amphipoda	-23.1+/-0.4(3)	8.3+/-0.1(3)	-24.1+/-2.5(2)	7.3+/-0.3(2)
Other				
Chironomidae larvae	na	na	na	na
Profundal/Pelagic Invertebrates				
Corixidae	-23.2	9.3		
Amphipoda	-27.1	8.9	-26.0	7.8
Chaoboridae larvae	-23.4	10.2	-26.7	9.4
Chaoboridae pupae	na	na	na	na
Chironomidae larvae	-25.9	8.5	-23.4	7.1
Daphnidae	na	na	-24.6+/-0.2(2)	5.6+/-0.6(2)
Hydrachnidia	-23.5	8.7		
zooplankton x>243 µm	-22.8+/-0.0(2)	6.1+/-1.5(3)	-22.4	4.6

Table D2: Isotopic signatures ((mean+/- *SE*)(n) or single values (‰)) of primary producers in LLB800 during summer 1996.

	May		June	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
phytoplankton x<250 µm	26.9	6.7	na	na
phytoplankton x>250 µm	na	na	na	na
POM	-27.4	14.4	-24.8+/-0.4(4)	7.0+/-0.4(4)
Lemna trisulca	-17.2	8	-16.8	9.0
Lemna minor	na	na	na	na
Myriophyllum sp.	-16.0	5.1	na	na
Nostoc sp.	na	na	-8.2	0.9
Nuphar sp.	na	na	-22.2	7.3
Potamogeton gramineus	na	na	-26.3	6.3
Potamogeon richardsonii	na	na	-11.8	5.9
Potamogeton zosteriformis	na	na	na	na
Potamogeton pusillus	na	na	na	na
Ceratophyllum sp.	na	na	na	na
Chara sp.	na	na	na	na
Gloeotrichia sp.	na	na	-23.2+/-0.1(6)	7.1+/-0.3(6)
Sagittaria sp.	-26.3	4.4	na	na
Equisetum sp.	-25.8	3.6	na	na
Typha sp.	-29.2	6.7	na	na
Juncus sp.	na	na	na	na
littoral detritus	-25.8	5.1	na	na
profundal detritus	-29.7+/-0.1(2)	3.1+/-0.5(2)	-29.5+/-0.0(2)	4.9+/-0.2(2)
terrestrial matter	na	na	na	na

Table D2: (continued)

Organism	August		September	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
phytoplankton x<250 µm	-25.3+/-1.4(3)	3.5+/-0.1(3)	na	na
phytoplankton x>250 µm	-18.1+/-0.3(3)	3.9+/-0.1(3)	na	na
POM	-23.6	3.4	na	na
Lemna trisulca	-20.9	7.7	-26.2+/-0.0(2)	4.1+/-0.1(2)
Lemna minor	na	na	-26.8	6.5
Myriophyllum sp.	na	na	-21.4	4.3
Nostoc sp.	-15.6+/-1.4(2)	2.7+/-0.4(2)	na	na
Nuphar sp.	-24.3	7.2	-23.7	4.5
Potamogeton gramineus	na	na	na	na
Potamogeon richardsonii	-13.1	10.0	-13.6+/-0.3(2)	7.6+/-0.6(2)
Potamogeton zosteriformis	na	na	-15.0	4.3
Potamogeton pusillus	na	na	-27.1	1.0
Ceratophyllum sp.	-17.5	7.4	na	na
Chara sp.	-25.8	5.6	na	na
Gloeotrichia sp.	-20.4	3.9	na	na
Sagittaria sp.	-25.1	7.9	-25.7	5
Equisetum sp.	na	na	-26.0	7.5
Typha sp.	na	na	-29.1	8.5
Juncus sp.	na	na	-28.0	5.8
littoral detritus	-26.1	3.8	-25.1	2.6
profundal detritus	-29.4+/-0.1(2)	4.8+/-0.1(2)	-29.8+/-0.1(2)	3.1+/-0.3(2)
terrestrial matter	na	na	na	na

Appendix E:

Isotopic signatures of biota in SCL20 and LLB800 during summer 1995

Table E1: Isotopic signatures ((mean+/-SE)(n) or single values (‰)) of biota in SCL20 and LLB800 during August 1995.

	SCL 20		LLB 800	
Organism	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Fish				
Northern pike	na	na	-24.3+/-0.2(2)	13.6+/-0.9
Yellow perch	na	na	-19.9	12.6
White sucker	na	na	-25.4	12.3
Fathead minnow	-26.5 +/- 0.3(3)	12.5 +/- 0.6(3)	na	na
Littoral invertebrates				
Amphipoda	-23.2	5.4	-18.3	6.4
Corixidae	-22.1	3.4	na	na
Hydrophilidae	na	na	-28.5	6.3
Gastropoda	na	na	-12.2	3.7
Gyrinidae	na	na	-23.9	6.9
Hirudinea	-26.6	8.9	-21.5	10
Notonectidae	na	6.6 +/- 0.3(2)	-23	8.9
Oligochaetae	na	na	-21	6.2
Trichoptera larvae	-25.2	6.3	na	7.8
Zygoptera	na	na	na	na
Pelagic invertebrates				
Chaoboridae larvae	na	na	-27.6	9.2
zooplankton	na	11.3	na	na
Primary producers				
POM	-29.9	6.6	-14.6	2.7
epiphytes	-26.8	10	na	na
Equisetum sp.	-28.5	4.7	-28.6	7.1
Lemna sp.	na	na	-18.2	7.8
Nostoc sp.	na	na	-8.75 +/- 2.5(2)	-0.1 +/- 0.7(2)
Nuphar sp.	-24.2	-1.7	-24.3	8.7
Polygonum sp.	-27.4	6	-29.9	4.5
Potamogeton sp.	-14.7	6	-12.6	5.8
Potamogeton sp.	na	na	-13.4	2.7
Sagittaria sp.	na	na	-24.3	6.2
Typha sp.	-26.9	na	-28.2	7.4
Scirpus sp.	na	na	-29.2	6.1
littoral detritus	-28.3	2.4	na	na
profundal detritus	-29.4	4	-29.1	3.8
alder	-29.9	-1.4	-29	0
aspen	-28.5	-0.4	na	na
balsam poplar	-27.8	-0.7	-28.7	0.2
birch	-28.6	na	-29.2	0.2
humus	-28	1.1	-28.4	2
litter	-28.2	-1.9	-27.6	0.7
spruce	-18.5	-1.9	-17.7	na

Appendix F:

$\delta^{13}C$ of dissolved inorganic carbon of lakewater collected at various depths in the study lakes

Table F1: $\delta^{13}C$ (‰) of dissolved inorganic carbon of lakewater collected at various depths in the study lakes.

Month	Lake	Depth (m)	$\delta^{13}C$
May	LLB800	1	-6.27
		5	-6.28
	SCL20	7	-3.84
		1.5	-2.96
	SPH200	5.5	-6.88
		1	-2.95
June	LLB800	5.5	-6.17
		2	-4.31
	SCL20	8.5	-5.48
		3	-2.89
	SPH200	7	-7.26
		2.5	-3.76
August	LLB800	1	-7.46
		6	-8.36
	SCL20	7	-5.81
		2.75	-4.13
	SPH200	7	-10.58
		1	-4.05
	SPH20	1	-3.35
		7	-5.55
September	LLB800	1	-7.91
		5	-8.40
	SCL20	7.75	-5.51
		2.75	-4.07
	SPH200	0	-5.16
	LLB20	1	-7.65
		4	-8.05
	C17	4	-9.79
		0	-11.52
	R4	4	-13.64
		0	-13.22

Appendix G:

Isotopic signatures of fish in SCL20, SPH200, LLB20, SPH20, C17 and R4 during summer 1996

Table G1: Isotopic signatures (‰) of fish in SCL20 during summer 1996.

Month	Species	Length	$\delta^{13}C$	$\delta^{15}N$
May	Fathead minnow	51	-27.84	13.90
	Fathead minnow	60	-27.42	13.32
	Fathead minnow	55	-28.52	13.89
	Fathead minnow	44	-28.57	14.60
	Fathead minnow	61	-27.90	13.49
June	Fathead minnow	42	-28.47	15.41
	Fathead minnow	47	-28.92	15.47
	Fathead minnow	50	-29.45	14.05
	Fathead minnow	62	-29.45	14.17
	Fathead minnow	57	-30.25	13.26
August	Fathead minnow	68	-28.54	13.63
	Fathead minnow	64	-27.06	14.11
	Fathead minnow	60	-28.24	14.46
	Fathead minnow	58	-27.01	13.90
	Fathead minnow	55	-27.71	14.39
	Fathead minnow	46	-27.03	14.07
	Fathead minnow	43	-26.09	13.24
	Fathead minnow	40	-26.62	13.78
	Fathead minnow	37	-27.33	13.58
	Fathead minnow	35	-25.81	13.56
	Fathead minnow	30	-25.61	13.89
	Fathead minnow	30	-24.90	12.16
	Fathead minnow	29	-26.28	13.41
	Fathead minnow	28	-25.73	13.20
	Fathead minnow	28	-24.72	13.03
	Fathead minnow	28	-25.88	13.41
	Fathead minnow	26	-25.69	13.26
	Fathead minnow	26	-25.36	13.45
	Fathead minnow	25	-25.59	12.93
	Fathead minnow	24	-25.12	13.39
	Fathead minnow	24	-25.34	13.45
	Fathead minnow	24	-25.13	13.64
	Fathead minnow	23	-24.85	13.20
	Fathead minnow	22	-25.41	13.43
	Fathead minnow	22	-25.50	14.29
	Fathead minnow	22	-25.14	13.22
	Fathead minnow	21	-24.84	12.43
	Fathead minnow	21	-24.78	13.28
	Fathead minnow	20	-25.10	12.96
	Fathead minnow	18	-25.05	13.19
September	Fathead minnow	64	-27.09	13.96
	Fathead minnow	74	-26.98	13.86
	Fathead minnow	35	-26.70	14.09
	Fathead minnow	45	-26.72	12.96

Table G2: Isotopic signatures (‰) of fish in SPH200 during summer 1996.

Month	Species	Length	$\delta^{13}C$	$\delta^{15}N$
May	N. pike	540	-27.50	12.24
June	N. pike	325	-26.99	10.79
	N. pike	215	-28.33	11.04
	N. pike	425	-27.45	11.87
	N. pike	820	-27.00	12.28
	N. pike	930	-26.20	13.81
	N. pike	558	-27.43	10.90
	N. pike	51	-27.29	8.73
	N. pike	60	-26.22	8.91
	N. pike	49	-26.86	9.18
	N. pike	50	-28.48	9.34
	N. pike	58	-26.73	9.63
	Br. stickleback	12	-29.61	11.20
	Br. stickleback	15	-29.99	11.65
	Br. stickleback	17	-30.50	11.68
July	Br. stickleback	42	-29.46	11.42
August	N. pike	730	-26.55	13.54
	N. pike	564	-28.85	12.24
	N. pike	562	-28.33	12.29
	N. pike	504	-28.63	12.36
	N. pike	405	-27.13	10.94
	N. pike	386	-28.00	10.85
	N. pike	334	-27.36	11.67
	N. pike	333	-26.76	10.90
	N. pike	306	-26.90	11.05
	N. pike	274	-26.47	10.10
	N. pike	173	-28.93	13.32
	N. pike	160	-26.26	11.35
	N. pike	142	-25.92	9.02
	N. pike	136	-28.86	13.15
	N. pike	134	-26.35	10.49
	N. pike	133	-25.27	10.65
	N. pike	127	-28.41	13.17
	N. pike	126	-24.79	9.98
	N. pike	125	-24.10	8.89
	N. pike	123	-25.98	11.36
	N. pike	119	-24.93	9.83
	N. pike	113	-25.14	9.18

Table G3: Isotopic signatures (‰) of fish in LLB20 during summer 1996.

Month	Species	Length (mm)	$\delta^{13}C$	$\delta^{15}N$
September	N. pike	768	-24.71	13.27
	N. pike	648	-31.38	10.11
	N. pike	520	-28.74	11.07
	N. pike	482	-25.64	13.14
	N. pike	476	-23.97	14.13
	N. pike	452	-30.95	8.54
	N. pike	444	-24.50	14.82
	N. pike	427	-25.23	11.86
	N. pike	396	-25.77	13.59
	N. pike	361	-29.14	11.19
	N. pike	328	-27.21	13.63
	N. pike	311	-28.08	11.95
	N. pike	149	-27.30	12.93
	N. pike	148	-26.95	11.93
	N. pike	138	-26.42	12.31
	N. pike	126	-26.64	12.04
	N. pike	113	-25.97	13.37
	N. pike	109	-26.83	12.97
	Y. perch	327	-26.87	10.84
	Y. perch	314	-27.33	11.12
	Y. perch	302	-27.06	11.46
	Y. perch	264	-27.03	10.96
	Y. perch	256	-28.15	10.33
	Y. perch	156	-26.46	12.69
	Y. perch	136	-28.56	10.66
	Y. perch	133	-26.25	12.71
	Y. perch	128	-27.23	12.24
	Y. perch	116	-27.88	12.96
	Y. perch	79	-29.11	14.05
	Y. perch	77	-28.99	13.33
	Y. perch	76	-28.97	14.26
	Y. perch	74	-29.19	13.68
	Y. perch	73	-28.75	13.89
	Y. perch	66	-28.97	13.44
	Y. perch	64	-31.50	9.82

Table G4: Isotopic signatures (‰) of fish in SPH20 during summer 1996.

Month	Species	Length (mm)	$\delta^{13}C$	$\delta^{15}N$
August	N. pike	572	-25.82	17.14
	N. pike	651	-25.87	17.20
	N. pike	609	-24.96	16.88
	N. pike	577	-25.43	17.12
	N. pike	575	-26.41	17.65
	N. pike	572	-22.03	17.74
	N. pike	554	-25.71	17.05
	N. pike	536	-26.18	17.09
	N. pike	529	-26.10	17.18
	N. pike	505	-25.22	16.90
	N. pike	458	-25.94	16.78
	N. pike	411	-25.85	17.81
	N. pike	359	-25.42	17.15
	N. pike	261	-24.92	15.98
	W. sucker	437	-24.88	13.66
	W. sucker	508	-27.22	15.78
	Y. perch	142	-27.98	15.57
	Y. perch	126	-28.38	17.17
	Y. perch	125	-28.33	16.30
	Y. perch	83	-28.40	16.98
	Y. perch	82	-28.28	16.96
	Y. perch	80	-28.18	16.60
	Y. perch	78	-28.53	17.57
	Y. perch	74	-28.02	16.76
	Y. perch	71	-27.64	16.06
	Y. perch	68	-27.54	16.05
	Y. perch	52	-27.39	17.46
	Y. perch	82	-28.26	16.90

Table G5: Isotopic signatures (‰) of fish in C17 during summer 1996.

Month	Fish	Length (mm)	$\delta^{13}C$	$\delta^{15}N$
August	N. pike	99	-27.91	13.11
	N. pike	101	-27.82	11.00
	N. pike	107	-28.58	12.95
	N. pike	112	-28.23	12.69
	N. pike	114	-27.79	12.33
	N. pike	123	-27.86	12.49
	N. pike	126	-28.46	12.37
	N. pike	129	-27.92	12.64
	N. pike	130	-28.52	13.03
	N. pike	269	-27.26	13.04
	N. pike	329	-26.01	12.92
	N. pike	372	-27.01	12.88
	N. pike	421	-26.06	12.51
	N. pike	469	-26.73	13.16
	N. pike	475	-24.98	11.92
	N. pike	516	-27.14	13.22
	N. pike	534	-26.97	13.54
	N. pike	534	-26.61	13.91
	N. pike	570	-27.09	12.99

Table G6: Isotopic signatures (‰) of fish in R4 during summer 1996.

Month	Fish	Length (mm)	$\delta^{13}C$	$\delta^{15}N$
August	N. pike	140	-34.41	8.99
	N. pike	342	-31.92	10.20
	N. pike	347	-32.51	10.16
	N. pike	354	-31.64	10.53
	N. pike	367	-31.73	10.10
	N. pike	370	-31.83	10.26
	N. pike	374	-32.16	10.04
	N. pike	384	-32.22	9.95
	N. pike	459	-30.18	10.86
	N. pike	531	-30.76	10.84

Appendix H:

Water residence times of LLB800, SCL20, SPH200, LLB20 and SPH20

Table H1: Water residence times (WRT) of LLB800, SCL20, SPH200, LLB20, and SPH20.

Lake	Longterm mean of WRT (yr)	WRT (yr) in 1995	WRT (yr) in 1996
LLB800	15.5	12.9	3.1
SCL20	3.9	5.9	1.5
SPH200	1.9	2.8	0.7
LLB20	5.4	5.1	1.4
SPH20	6.7	10	2.3

$$\text{Water residence time} = \frac{\text{volume of water in lake } (m^3)}{\text{outflow } (m^3/yr)}$$

$$\text{Outflow per unit area} = \text{precipitation } (m*m^2/yr) + \text{runoff } (m*m^2/yr) - \text{evaporation } (m*m^2/yr)$$

Precipitation was regional measurements obtained from Water Survey Canada.
Runoff (unit area runoff) = Total discharge/area of drainage basin
Evaporation was calculated from Thornthwaite's equation.

Appendix I:

Predicted winter oxygen depletion rates (WODR) and estimated length of time (t_{crit}) it takes for hypoxic conditions to occur in LLB800, SCL20, SPH200, LLB20 and SPH20

Table I1: Predicted winter oxygen depletion rates (WODR) and estimated length of time (t_{crit}) it takes for hypoxic conditions to occur in LLB800, SCL20, SPH200, LLB20 and SPH20 based on Babin and Prepas (1985) model.

Year	Lake	Altitude* (m)	Water temperature (°C)	Initial** DO storage (mg/L)	Initial** DO Storage (mg/m2)	Mean depth (m)	Summer TP_{eu} (mg/m2)	Predicted WODR (mg/m2/d)	t_{crit} (days)
1995	LLB800	~544	4	12.1	36.4	3.0	154.0	0.32	114
	SCL20	~600	4	11.9	58.1	4.9	121.3	0.26	220
	SPH200	~577	4	12.1	49.4	4.1	121.9	0.26	194
	LLB20	~544	4	12.1	25.5	2.1	121.6	0.23	112
	SPH20	~577	4	12.1	53.0	4.4	113.2	0.24	223
1996	LLB800	~544	4	12.1	36.4	3.0	151.7	0.31	116
	SCL20	~600	4	11.9	58.1	4.9	152.9	0.34	170
	SPH200	~577	4	12.1	49.4	4.1	124.4	0.26	189
	LLB20	~544	4	12.1	25.5	2.1	119.6	0.22	115
	SPH20	~577	4	12.1	53.0	4.4	95.1	0.19	275

* altitudes of study lakes are approximates based on altitudes of larger lakes in the same region (Mitchell and Prepas 1991)

** assumes water is 100% saturated with dissolved oxygen

Appendix J:

Stomach content analysis (% frequency of occurrence and % number) of yellow perch in LLB20 and SPH20 during summer 1996

Table J1: Stomach content analysis (% frequency of occurrence and % number) of yellow perch in LLB20 and SPH20 during summer 1996.

Lake	Item	% FO	% number
LLB20	Amphipoda	73.3	29.3
n=15	Anisoptera larvae	6.7	0.1
yp>150mm	Chaoboridae larvae	6.7	0.2
	Chironomidae larvae	40.0	69.0
	Coleoptera larvae	6.7	0.1
	Notonectidae	20.0	0.9
	Pelycopoda	6.7	0.1
	Zygoptera	13.3	0.2
	unidentified invertebrate	13.3	0.2
n=6	Amphipoda	83.3	77.6
yp≤150mm	Chironomidae larvae	33.3	4.9
	Cladocera	16.7	3.5
	Coleoptera larvae	16.7	0.4
	Copepoda	16.7	13.6
	macrophytes	16.7	
	filamentous algae	16.7	
	fin part	16.7	
SPH20	Amphipoda	75.0	17.2
n=12	Chaoboridae larvae	83.3	58.1
yp≤150mm	Chironomidae larvae	41.7	1.6
	Cladocera	25.0	21.4
	Coleoptera larvae	16.7	0.7
	Notonectidae	8.3	0.3
	Nematoda	8.3	0.3
	unidentified invertebrate	8.3	0.3